Life history invariants of lean and siscowet lake trout, lake whitefish, bloater, walleye and yellow perch populations in the Great Lakes

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by

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ABSTRACT

Chu, C., and M.A. Koops. 2007. Life history invariants of lean and siscowet lake trout, lake whitefish, bloater, walleye and yellow perch populations in the Great Lakes. Can. Manuscr. Rep. Fish. Aquat. Sci. 2816: viii + 38p.

Life history invariants are symmetries in the trade-offs among life history traits where a change in one trait produces a predictable change in another life history trait. The excellent fits of proposed life history invariants to interspecific data has encouraged the use of proposed invariants in fisheries management and modelling. However, the few published intraspecific comparisons have been inconsistent in their support of proposed invariants. This study estimates life history invariants for populations of five fishes within the Great Lakes and within populations through time. Our analyses included 12 lean and 6 siscowet lake trout (*Salvelinus namaycush*), 26 lake whitefish (*Coregonus clupeaformis*), 8 bloater (*Coregonus hoyi*), 9 walleye (*Sander vitreus*), and 12 yellow perch (*Perca flavescens*) populations. Growth, maturity and population location data were gathered for each population. These data were used to calculate eight life history parameters (k, L_∞, t_0, L_0, α, L_α, M and t_{max}) and eight life history invariants (1^{st} Beverton-Holt, 2^{nd} Beverton-Holt, 3^{rd} Beverton-Holt, Roff, Hoenig, Charnov-Berrigan, Jensen and Mangel). Our results indicate that for all of these species, invariant values vary both among populations and within populations through time. The 2^{nd} and 3^{rd} Beverton-Holt invariants appeared to vary the least of the invariants tested but our results suggest that caution should be used when applying life history invariants to modelling exercises and fisheries management.

RÉSUMÉ

Chu, C., and M.A. Koops. 2007. Life history invariants of lean and siscowet lake trout, lake whitefish, bloater, walleye and yellow perch populations in the Great Lakes. Can. Manuscr. Rep. Fish. Aquat. Sci. 2816: viii + 38p.

Les invariants du cycle biologique sont des symétries dans les compromis entre caractères du cycle biologique, dans lesquelles le changement d'un caractère entraîne un changement prévisible d'un autre caractère. Les excellents ajustements d'invariants du cycle biologique proposés à des données interspécifiques ont encouragé l'utilisation de ces invariants dans la gestion et la modélisation des pêches. Cependant, les quelques comparaisons intraspécifiques publiées ne sont pas toutes arrivées aux mêmes conclusions quant à la pertinence des invariants proposés. La présente étude estime des invariants du cycle biologique entre des populations de cinq poissons dans les Grands Lacs, et à l'intérieur des populations dans le temps. Nos analyses ont porté sur 12 populations de touladi maigre, 6 populations de siscowet (touladi gras), 26 populations de grand corégone, 8 populations de cisco de fumage, 9 populations de doré jaune et 12 populations de perchaude. Des données sur la croissance, la maturité et la localisation géographique ont été recueillies pour chaque population. Ces données ont été utilisées pour calculer huit paramètres du cycle biologique (k, L_∞, t_0, L_0, α, L_α, M et t_{max}) et huit invariants du cycle biologique (1^{er}, 2^e et 3^e invariants de Beverton-Holt, et invariants de Roff, Hoenig, Charnov-Berrigan, Jensen et Mangel). Nos résultats indiquent que pour toutes ces espèces, les valeurs des invariants varient tant entre populations qu'au sein des populations dans le temps. De tous les invariants examinés, ce sont les 2^e et 3^e invariants de Beverton-Holt qui ont montré les plus faibles variations. Il reste que nos résultats laissent entendre qu'il faut être prudent quand on utilise des invariants du cycle biologique dans les exercices de modélisation et la gestion des pêches.

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INTRODUCTION

Life history invariants represent similarities in life history strategies of organisms (Charnov 1993; de Jong, 2005). They assume a change in one life history trait produces a constant, predictable change in another life history trait. For example, the 2nd Beverton-Holt Invariant assumes that there is a constant relationship between length at maturity and asymptotic length such that species that mature early are ultimately smaller than species that mature later in life (Beverton and Holt, 1959). Life history invariants can represent not only maturity but also growth and mortality parameters of organisms (Charnov and Berringan, 1991; Jensen, 1996). They are attractive for their utility in predicting the values of life history traits for which data are lacking or difficult to acquire, and their consistency across species has supported the utility of life history invariants in life history evolution theory (de Jong, 2005).

Particular attention has been given to estimating mortality from life history traits because mortality directly influences population dynamics and fisheries management decisions (Beverton and Holt, 1959; Pauly, 1980; Hoenig, 1983, Roff, 1984; Charnov *et al.*, 1993). Invariants have been tested using large amounts of interspecific data (Charnov, 1993; Charnov *et al.*, 1993; Froese and Binohlan, 2000), and the close fit of the results to the proposed invariant values has encouraged the use of proposed invariants in both fisheries management and modelling. However, the few published intraspecific comparisons have been inconsistent in their support of proposed invariants (Vøllestad *et al.*, 1993; Vøllestad and L'Abée-Lund, 1994; Mangel, 1996). The analyses used to calculate the invariant values and overall validity of invariants have recently been called into question (Nee *et al.*, 2005; de Jong, 2005).

We tested the applicability of life history invariants among populations of fishes within the Great Lakes and within populations through time. The objectives of this study were three-fold; the amalgamation of life history data for several fishes in the Great Lakes into a single database,

calculation of life history parameters and invariant values and an examination of interpopulation (spatial) and intrapopulation (temporal) trends in the invariant data. This report documents the data and methods used to calculate the life history invariants, and summarizes the calculated life history invariants for each species.

METHODS

DATA SOURCES

Individual fish data consisting of total length (cm), round weight (g), age (years), maturity (yes/no), sex (male, female or unknown), population code, population location and year sampled were gathered from several agencies throughout the Great Lakes (Table 1). Maturity data were not available for all populations. Fishes that were not aged were not included in our analyses. Population distinctions were based on historical information, tracking and spawning data. In total, aged data were available for 41,394 lean and 8,815 siscowet lake trout (*Salvelinus namaycush*), 48,565 lake whitefish (*Coregonus clupeaformis*), 25,875 bloater (*Coregonus hoyi*), 18,505 walleye (*Sander vitreus*), and 73,304 yellow perch (*Perca flavescens*) in the Great Lakes basin (Table 1). Yearly data spanned the early 1970's to 2003 but were not consistently available every year (Table 2).

Locations of populations for each species were compiled in ArcView 3.2 (ESRI, 1996). Lean lake trout data exist for Lake Superior and Lake Huron however siscowet lake trout data were only available for populations in Lake Superior (Figure 1). Lake whitefish data were available from each Great Lake and bloater data were available in lakes Michigan and Huron (Figure 2). Yellow perch data were available for all of the Great Lakes and data were available for walleye populations in lakes Huron, Erie and Ontario (Figure 3). Species data from Lake Ontario were not divided into different populations because population boundaries are not known for that lake (personal communication, J. Dietrich, OMNR).

Much of the data used in this study came from fishes caught using gillnet gangs of different mesh sizes. This sampling method is size selective with smaller meshes excluding large individuals and larger meshes excluding small individuals. Therefore growth curves fitted to these data may underestimate growth in older fish while inflating the growth rates of younger fish (Beauchamp *et al.*, 2004; Taylor *et al.*, 2005). Previous analyses indicated that pooling the data from different mesh sizes produced growth curves that were representative of mean population growth (Chu and Koops, 2007).

LIFE HISTORY PARAMETERS AND INVARIANTS

Eight life history parameters (Table 3) and eight life history invariants (Table 4) were calculated for each population with age, length and maturity data. For populations without maturity data (Table 1), only five life history parameters (k, L_0, t_0, t_{max}, M) and three invariants (1st Beverton-Holt invariant, 3rd Beverton-Holt invariant, Hoenig's Rule) were calculated. Asymptotic length, von Bertalanffy growth coefficient, age at length zero and length at age zero were calculated by fitting the length at age data to a von Bertalanffy growth function using Ford-Walford plots. Mortality was calculated using the catch-curve analysis outlined in Hilborn and Walters (1992) with the catch at age data.

VIRTUAL POPULATION ANALYSES

Virtual population analyses (VPA) were also used in this study. This approach differs from the inter- and intra-population analyses because it estimates the life history parameters and invariants of individual cohorts rather than the mean of the populations or means of individual years. Populations with at least 10 consecutive years of data were used for these analyses. This included 10 populations, EWAL1, EWAL2, EYP1, EYP2, HLWFON2, HYPON2, OLWF1, OYP1, SLTSISMI7 and SLTWI2 (Table 2).

RESULTS

INTERPOPULATION LIFE HISTORY INVARIANT ANALYSES

This section focuses on the invariant results for the lean lake trout, siscowet lake trout, lake whitefish, bloater, walleye and yellow perch populations (Tables 5-9). The life history parameters are summarized in Chu and Koops (2007). All of the proposed invariants were within the range observed for lean lake trout (Figure 4). The proposed Hoenig value was greater than the observed invariant values of the siscowet lake trout populations in Lake Superior (Figure 4). All of the proposed invariant values were within the range of values calculated for lake whitefish (Figure 5). The Charnov-Berrigan proposed value was the only invariant greater than the range of values observed for the bloater (Figure 5) and yellow perch (Figure 6) populations. The Charnov-Berrigan invariant was at the upper limit of invariant values calculated for the walleye populations (Figure 6).

The 2nd and 3rd Beverton-Holt invariants varied little relative to the other invariants. The Roff invariant values ranged the most among the lean and siscowet lake trout, lake whitefish and yellow perch populations while the Hoenig invariant varied the most for bloater and walleye populations. The calculated invariant values for all eight invariants varied the least among the yellow perch populations, and the most, among the bloater populations.

INTRAPOPULATION LIFE HISTORY INVARIANT ANALYSES

The invariant values for populations through time are summarized in Tables 5-9. Some years of data were omitted if <10 fish of a species were caught, all fish caught were either immature or mature or if fish caught belonged to only one or two age classes (therefore growth curves could not be derived from the data).

For easier interpretation, the 3rd Beverton-Holt (3BHI) and the Charnov-Berrigan (C-B) invariant are presented for the longest available time series of data for each species. Invariant

values for the SLTMI4 population of lake trout in Lake Superior ranged from -0.5 to 0.0 throughout the 1971-2003 period with a peak in the late 1980's. The C-B invariant varied between 2 and 6 throughout the time period (Figure 7). The 3BHI invariant values for the SLTSISMI7 siscowet lake trout population increased from 1995-2004. The C-B invariant varied around 1 with a decline since 2001 (Figure 7). The 3BHI values declined for lake whitefish through time and showed no discernable pattern for bloater. The C-B values varied little compared to the 3BHI and were consistently lower than the proposed value throughout the time series (Figure 8). The Lake Erie walleye and yellow perch populations also showed a decline in the 3BHI invariant but there was no consistent increase or decrease in the C-B invariant (Figure 9).

The 3BHI and C-B invariants varied for all of the populations through time. The observed 3BHI values were greater than the proposed for most of the lean lake trout, lake whitefish and walleye time series. 3BHI values fluctuated around the proposed value in the siscowet lake trout, yellow perch and bloater populations. The C-B invariant values were less than the proposed value in the siscowet lake trout, walleye, yellow perch and bloater populations. The lean lake trout and lake whitefish values fluctuated around the proposed value throughout the time series.

VIRTUAL POPULATION ANALYSES

Life history invariants varied for all cohorts (Table 10). Maturity data were not available for the lake whitefish cohorts in Lake Ontario so only the 1BHI, 3BHI and Hoenig invariants were calculated. Lake whitefish cohorts from Lake Ontario had 1BHI and 3BHI values closer to the proposed values than the Lake Huron cohorts. The Hoenig values for the Lake Huron cohorts were closer to the proposed value than the Lake Ontario cohorts. The walleye cohorts

from the E1 and E2 populations in Lake Erie had invariant values within the same range. There was no clear distinction among the invariant values calculated for yellow perch cohorts in lakes Erie, Huron and Ontario. The 2BHI, Roff, Hoenig, C-B, and Mangel invariants values for the walleye and yellow perch cohorts were consistently lower than the proposed values (Table 10).

DISCUSSION

Our findings suggest that life history invariants do indeed vary among populations of the same species and within populations through time. These findings are consistent with recent publications documenting variations in life history parameters of fishes such as lake trout (Shuter *et al.*, 1998), walleye (Lester *et al.*, 2000) and yellow perch (Purchase *et al.*, 2005).

Nee *et al.* (2005) suggest that the data supporting life history invariants are erroneous because life history parameters are generated by regressing a variable against a fraction of itself. This produces regressions with high R^2 values and a misunderstanding that model slopes that are not significantly different from 1 are invariant. de Jong (2005) also demonstrates that it is not only the regression of related variables against each other that produces slopes close to 1 but also the use of log-log plots that removes the variability in the data to produce slopes close to 1, i.e. invariance. These criticisms suggest that direct comparison between data and proposed values is the most appropriate way to test life history invariants.

The spatial and temporal variation in life history invariants in the Great Lakes may be due to regional factors such as climate, and local factors such as lake size. Temperature affects the growth of fishes and may directly or indirectly affect their mortality. Fish living in different thermal habitats may exhibit very different life history parameters that translate into different invariant values. At a local scale, variation in early growth rate and female maximum size were positively related to lake surface area and water hardness, respectively, for yellow perch

populations in Ontario (Purchase *et al.*, 2005). Density-dependent growth also explained variance in intrapopulation growth parameters of bloater in Lake Michigan (Szalai *et al.*, 2003).

Our findings suggest that researchers should exercise caution when applying invariants to modelling and management practices in the Great Lakes Basin until further investigation. The 2nd and 3rd Beverton-Holt invariants varied the least of the invariants examined in the interpopulation comparisons but none of the invariants appeared to perform well at the intrapopulation level.

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Table 1. Summary of the interpopulation data used to examine the life history parameters of fish populations in the Great Lakes Basin. Population codes correspond to Figures 1-3. Lake trout, yellow perch and bloater were aged using scales, siscowet lake trout, lake whitefish and walleye with otoliths.

Species	Lake	Populations	Number of fish	Age	TL	RWT	SEX	MAT	Source
Lake trout lean	Huron	HLTON1	2988	X	X	X	X	X	Mohr, OMNR
		HLTON2	140						
	Superior	SLTWI1	3619	X	X	X	X	X*	Seider, WIDNR;
		SLTWI2	13967						Sitar, MDNR;
		SLTMI2	469						Ebener, CORA;
		SLTMI3	1230						MacIntosh,
		SLTMI4	3203						OMNR
		SLTMI5	2448						
		SLTMI6	1611						
		SLTMI7	1293						
		SLTON1	10426						
Lake trout siscowet	Superior	SLTSISMI2	493	X	X	X	X	X	Sitar, MDNR;
		SLTSISMI3	2255						Ebener, CORA
		SLTSISMI4	2254						
		SLTSISMI5	1900						
		SLTSISMI6	978						
		SLTSISMI7	935						
Lake whitefish	Erie	ELWF1	14	X	X	X	X	X	Johnson, OMNR
		ELWF2	279						
		ELWF3	233						
		ELWF4	107						
		ELWF7	113						
	Ontario	OLWF1	2381	X	X	X	X		Dietrich, OMNR
	Huron	HLWFON1	6527	X	X	X	X	X	Mohr, OMNR
		HLWFON2	9114						and Ebener,
		HLWFON3	351						CORA
		HLWFCORA5	593						
		HLWFCORA6	145						
		HLWFCORA8	213						
		HLWFCORA13	210						
	Michigan	MLWFCORA9	539	X	X	X	X	X	Ebener, CORA
		MLWFCORA10	1146						
		MLWFCORA12	52						
		MLWFCORA14	59						
	Superior	SLWFMI2	131	X	X	X	X	X*	Seider, WIDNR;
		SLWFMI3	840						Sitar, MDNR;
		SLWFMI4	28						Ebener, CORA;
		SLWFMI5	31						MacIntosh,
		SLWFMI6	257						OMNR
		SLWFMI7	1663						
		SLWFMI8	79						
		SLWFWI2	41						
		SLWFON1	23419						

Bloater	Michigan	MBLOMM1	1768	X	X	X	X	X	Clapp, MDNR
		MBLOMM3	5370						
		MBLOMM4	4037						
		MBLOMM5	2541						
		MBLOMM6	21						
	Huron	HBLOON1	5642	X	X	X	X	X	Mohr, OMNR
		HBLOON2	5538						
		HBLOON3	958						
Walleye	Erie	EWAL1	8439	X	X	X	X	X	Johnson, OMNR
		EWAL2	3991						
		EWAL3	1236						
		EWAL4	799						
		EWAL7	132						
	Ontario	OWAL1	3647	X	X	X	X		Dietrich, OMNR
	Huron	HWALLON1	14	X	X	X	X	X	Mohr, OMNR
		HWALLON2	208						
		HWALLON3	39						
Yellow perch	Erie	EYP1	11453	X	X	X	X	X	Johnson, OMNR
		EYP2	16946						
		EYP3	14622						
		EYP4	5648						
		EYP7	2201						
	Ontario	OYP1	4140	X	X	X	X		Dietrich, OMNR
	Huron	HYPON1	1929	X	X	X	X	X	Mohr, OMNR
		HYPON2	11064						
		HYPON3	874						
	Superior	SYPON1	1590	X	X	X	X		MacIntosh, OMNR
	Michigan	MYPMM1	2202	X	X	X	X	X	Clapp, MDNR
		MYPMM2	635						

* no maturity data for the OMNR and WIDNR datasets

Table 2. Summary of the intrapopulation (yearly) data used to calculate the life history parameters of fish populations through time. Population codes correspond to Figures 1-3.

Species	Population	Number of years	Years
Lake trout – lean	HLTON1	2	1990, 2003
Lake trout – lean	HLTON2	2	1990, 2003
Lake trout – lean	SLTWI1	14	1987-95, 19997-00, 2002
Lake trout – lean	SLTWI2	21	1981-95, 1997-00, 2002-03
Lake trout – lean	SLTMI2	8	1995-96, 1998-2003
Lake trout – lean	SLTMI3	11	1977, 1981, 1987, 1995-96, 1998-2003
Lake trout – lean	SLTMI4	18	1971-72, 1975, 1977, 1980-83, 1987, 1995-2003
Lake trout – lean	SLTMI5	14	1975, 1980-83, 1987, 1995-96, 1998-2003
Lake trout – lean	SLTMI6	15	1975, 1980-83, 1987, 1995-2003
Lake trout – lean	SLTMI7	12	1981, 1983, 1987, 1995-2003
Lake trout – lean	SLTMI8	3	1975, 1981, 1982
Lake trout – lean	SLTON1	8	1988-95
Lake trout – siscowet	SLTSISMI2	8	1995-96, 1998-03
Lake trout – siscowet	SLTSISMI3	8	1995-96, 1998-03
Lake trout – siscowet	SLTSISMI4	9	1995-03
Lake trout – siscowet	SLTSISMI5	9	1995-03
Lake trout – siscowet	SLTSISMI6	10	1980, 1983, 1995-96, 1998-03
Lake trout – siscowet	SLTSISMI7	10	1995-04
Lake whitefish	ELWF2	9	1995-03
Lake whitefish	ELWF3	6	1997-03
Lake whitefish	ELWF4	5	1989-91, 1998, 2002
Lake whitefish	ELWF7	4	1991, 1993, 1994, 1998
Lake whitefish	HLWFCORA13	2	2001-02
Lake whitefish	HLWFCORA5	7	1983, 1985-86, 2000-03
Lake whitefish	HLWFCORA6	4	2000-03
Lake whitefish	HLWFCORA8	3	1985, 2001-02
Lake whitefish	HLWFON1	13	1981-82, 1985-92, 2001-03
Lake whitefish	HLWFON2	15	1981-92, 2001-03
Lake whitefish	HLWFON3	7	1987-92, 2001, 2003
Lake whitefish	MLWFCORA9	2	2001-02
Lake whitefish	MLWFCORA10	4	2000-03
Lake whitefish	MLWFCORA14	2	2002-03
Lake whitefish	SLWFMI3	3	1995, 1998, 2003
Lake whitefish	SLWFMI6	4	1995, 1998, 2002, 2003
Lake whitefish	SLWFMI7	7	1981-84, 2001-03
Lake whitefish	SLWFMI8	3	2001-03
Lake whitefish	SLWFWI2	2	1991-92
Lake whitefish	OLWF1	13	1992-04
Lake whitefish	SLWFON1	7	1989, 1991-1996
Bloater	MBLOMM1	5	1980-82, 86, 88
Bloater	MBLOMM3	7	1980-83, 85, 86, 88
Bloater	MBLOMM4	5	1980-82, 84, 86
Bloater	MBLOMM5	7	1980-1986
Bloater	HBLOON1	6	1989, 1991-92, 2001-03
Bloater	HBLOON2	9	1986-87, 1989-92, 2001-03
Bloater	HBLOON3	6	1986-90, 1992
Walleye	EWAL1	13	1990, 1992-03
Walleye	EWAL2	13	1990, 1992-03

Walleye	EWAL3	11	1989-92, 1994-95, 1997-98, 2001-03
Walleye	EWAL4	11	1989-92, 1994, 1998-03
Walleye	EWAL7	9	1991-92, 1994-95, 1998-03
Walleye	HWALLON2	9	1984, 1987-91, 2001-03
Walleye	OWALL1	13	1992-04
Yellow perch	EYP1	13	1990, 1992-03
Yellow perch	EYP2	13	1990, 1992-03
Yellow perch	EYP3	14	1989-95, 1997-03
Yellow perch	EYP4	13	1989-95, 1998-03
Yellow perch	EYP7	11	1991-95, 1998-03
Yellow perch	HYPON1	8	1981, 1983, 1985, 1987-91
Yellow perch	HYPON2	15	1981-92, 01-03
Yellow perch	HYPON3	4	1988, 2001-03
Yellow perch	OYP1	13	1992-04
Yellow perch	SYPON1	6	1991-96
Yellow perch	MYPMM1	4	1986, 1996-1998
Yellow perch	MYPMM2	4	1980-1983

Table 3. Life history parameters calculated from age, length and maturity data from each species and population.

Life history parameter	Description
k	von Bertalanffy growth coefficient (yr^{-1})
L_∞	asymptotic length (cm)
t_0	age at length 0 (yr)
L_0	length at age 0 (cm)
α	age at maturity (yr)
L_α	length at maturity (cm)
Z	total mortality rate (yr^{-1})
t_{max}	maximum lifespan (yr)

Table 4. Life history invariants and proposed values of life history invariants used in this study.

Life history invariant	Abbrev.	Proposed value
1st Beverton-Holt invariant: Z/k	1-BHI	1.65
2nd Beverton-Holt invariant: L_α / L_∞	2-BHI	0.68-0.81 used 0.75
3rd Beverton-Holt invariant: slope of Ln k verus Ln L_∞	3-BHI	-0.5
Roff Invariant: $(Z/k)/(L_\infty / L_\alpha - 1)$	Roff	3
Hoenig's Rule: Zt_{max}	Hoenig	4.3
Charnov-Berrigan invariant: αZ	C-B	2
Jensen invariant: αk	Jensen	ln 3 = 1.0986
Mangel invariant: $\alpha k/Ln((Zc+3kc)/Z)$ where $c= \exp(k\ t_0)$	Mangel	1

Table 5. Intrapopulation and interpopulation (years pooled) life history invariant values for lake whitefish (LWF), walleye (WALL) and yellow perch (YP) populations in Lake Erie. Interpopulation invariants are highlighted with boxes. Population codes correspond to Figures 1-3.

Species	Population	Year	Fish	1-BHI	2-BHI	3-BHI	Roff	Hoenig	C-B	Jensen	Mangel
LWF	E1		14	0.33	0.82	0.02	1.50	2.45	1.40	4.25	1.07
LWF	E2	1995	28	0.47	0.69	-0.18	1.04	0.92	0.69	1.48	0.86
LWF	E2	1996	13	0.15	0.69	0.01	0.34	1.10	0.47	3.10	0.86
LWF	E2	1997	60	0.28	0.66	-0.06	0.56	2.19	0.66	2.30	0.60
LWF	E2	1998	22	0.10	0.64	0.06	0.18	1.02	0.26	2.51	0.43
LWF	E2	1999	43	0.23	0.78	-0.05	0.80	1.83	0.55	2.43	0.71
LWF	E2	2000	47	0.20	0.53	-0.09	0.23	1.66	0.28	1.37	0.30
LWF	E2	2002	17	0.37	0.76	-0.11	1.19	2.16	0.72	1.92	0.68
LWF	E2	2003	29	0.28	0.79	-0.17	1.01	1.10	0.55	2.00	0.68
LWF	E2		279	0.45	0.51	-0.17	0.48	2.72	0.68	1.49	0.53
LWF	E3	1997	114	0.44	0.58	-0.07	0.60	2.68	1.01	2.29	0.72
LWF	E3	1998	35	0.18	0.60	-0.04	0.27	1.41	0.31	1.71	0.41
LWF	E3	1999	23	0.42	0.78	-0.18	1.52	1.46	0.63	1.47	0.91
LWF	E3	2000	14	0.33	0.71	-0.13	0.80	0.99	0.60	1.83	0.76
LWF	E3	2002	14	0.70	0.71	-0.29	1.70	1.90	0.63	0.90	0.68
LWF	E3	2003	10	0.50	0.75	-0.34	1.51	0.65	0.52	1.04	0.77
LWF	E3		231	1.02	0.54	-0.34	1.17	2.29	0.51	0.50	0.51
LWF	E4	1989	10	0.24	0.98	0.10	14.33	1.75	1.40	5.82	1.81
LWF	E4	1990	13	0.11	0.65	0.26	0.21	1.23	0.61	5.58	0.87
LWF	E4	1991	13	0.06	0.68	-0.08	0.13	0.56	0.14	2.19	0.45
LWF	E4	1998	41	0.28	0.50	-0.24	0.28	0.82	0.20	0.74	0.32
LWF	E4	2002	10	0.54	0.72	-0.15	1.38	1.81	0.90	1.67	0.94
LWF	E4		107	0.61	0.50	-0.28	0.61	2.30	0.38	0.63	0.43
LWF	E7	1993	21	0.18	0.78	0.04	0.67	1.71	0.86	4.66	0.83
LWF	E7	1994	13	0.45	0.92	-0.17	5.54	1.63	0.70	1.54	0.90
LWF	E7	1998	47	0.55	0.75	-0.13	1.66	2.31	0.99	1.81	0.77
LWF	E7		113	0.34	0.70	-0.10	0.77	2.50	0.91	2.70	0.77
WALL	E1	1990	323	1.15	0.58	-0.34	1.59	1.92	0.55	0.48	0.58
WALL	E1	1992	554	0.42	0.49	-0.14	0.41	2.30	0.46	1.10	0.41
WALL	E1	1993	268	0.37	0.64	-0.12	0.66	2.27	0.68	1.84	0.64
WALL	E1	1994	872	0.85	0.55	-0.28	1.06	2.35	0.52	0.62	0.46
WALL	E1	1995	1444	0.54	0.69	-0.16	1.19	2.77	0.83	1.53	0.70
WALL	E1	1996	722	0.77	0.57	-0.33	1.00	2.26	0.56	0.74	0.52
WALL	E1	1997	872	0.66	0.59	-0.19	0.95	2.65	0.88	1.34	0.73
WALL	E1	1998	179	0.84	0.46	-0.37	0.73	1.87	0.34	0.40	0.32
WALL	E1	1999	575	0.54	0.62	-0.18	0.87	2.80	0.76	1.42	0.68
WALL	E1	2000	689	1.38	0.49	-0.44	1.34	2.63	0.44	0.32	0.60
WALL	E1	2001	418	0.45	0.44	-0.20	0.34	2.31	0.39	0.86	0.36
WALL	E1	2002	455	0.93	0.60	-0.34	1.42	2.34	0.47	0.50	0.65
WALL	E1	2003	1068	0.59	0.58	-0.26	0.81	2.90	0.58	0.99	0.46
WALL	E1		8439	1.74	0.48	-0.44	1.61	3.85	0.77	0.44	0.72
WALL	E2	1990	266	1.42	0.55	-0.25	1.76	3.40	0.97	0.68	0.77
WALL	E2	1992	619	1.04	0.55	-0.35	1.25	2.12	0.47	0.45	0.54
WALL	E2	1993	310	1.17	0.40	-0.40	0.78	2.05	0.41	0.35	0.41
WALL	E2	1994	271	0.98	0.56	-0.35	1.27	2.14	0.43	0.44	0.43
WALL	E2	1995	773	1.39	0.51	-0.38	1.46	3.47	0.53	0.39	0.56
WALL	E2	1996	460	1.36	0.48	-0.44	1.27	2.07	0.41	0.30	0.48
WALL	E2	1997	377	0.47	0.63	-0.22	0.81	1.86	0.37	0.80	0.44
WALL	E2	1998	71	0.23	0.55	-0.09	0.28	1.41	0.16	0.68	0.22
WALL	E2	1999	77	0.27	0.57	-0.27	0.35	0.69	0.17	0.64	0.28
WALL	E2	2000	319	0.73	0.48	-0.31	0.68	2.12	0.39	0.53	0.37

WALL	E2	2001	53	0.52	0.68	-0.27	1.08	1.35	0.34	0.65	0.55
WALL	E2	2002	160	0.77	0.64	-0.30	1.35	1.75	0.44	0.57	0.61
WALL	E2	2003	234	0.28	0.55	-0.14	0.33	1.98	0.30	1.10	0.31
WALL	E2		3991	1.48	0.40	-0.40	0.99	3.43	0.53	0.36	0.52
WALL	E3	1989	333	0.43	0.54	-0.09	0.50	2.93	0.59	1.37	0.42
WALL	E3	1990	68	0.28	0.55	-0.14	0.33	1.98	0.30	1.10	0.31
WALL	E3	1991	82	1.26	0.50	-0.26	1.28	2.96	0.42	0.33	0.40
WALL	E3	1992	129	0.55	0.50	-0.08	0.54	3.51	0.39	0.70	0.26
WALL	E3	1994	133	1.33	0.49	-0.27	1.28	4.24	0.85	0.64	0.64
WALL	E3	1995	146	1.53	0.54	-0.41	1.77	2.90	0.53	0.34	0.57
WALL	E3	1997	72	0.45	0.58	-0.34	0.63	1.22	0.30	0.68	0.38
WALL	E3	1998	26	0.21	0.53	-0.21	0.24	0.92	0.17	0.81	0.28
WALL	E3	2001	24	0.32	0.48	-0.39	0.29	0.60	0.06	0.19	0.10
WALL	E3	2002	90	0.32	0.54	-0.43	0.38	0.69	0.10	0.31	0.19
WALL	E3	2003	61	0.15	0.66	0.07	0.29	1.56	0.39	2.65	0.51
WALL	E3		1236	1.01	0.45	-0.38	0.84	2.96	0.39	0.39	0.37
WALL	E4	1989	150	1.06	0.62	-0.36	1.71	2.12	0.71	0.67	0.96
WALL	E4	1990	48	0.75	0.64	-0.28	1.31	1.67	0.48	0.63	0.52
WALL	E4	1991	23	0.36	0.70	-0.30	0.87	0.71	0.31	0.84	0.45
WALL	E4	1992	12	0.20	0.60	-0.19	0.30	0.53	0.18	0.90	0.32
WALL	E4	1994	21	0.99	0.66	-0.22	1.89	3.11	1.17	1.18	0.87
WALL	E4	1998	25	0.19	0.66	-0.16	0.36	1.25	0.29	1.54	0.40
WALL	E4	1999	89	1.28	0.49	-0.43	1.24	2.20	0.40	0.31	0.51
WALL	E4	2000	104	0.68	0.56	-0.31	0.86	2.34	0.36	0.53	0.35
WALL	E4	2001	117	0.06	0.50	-0.43	0.06	0.12	0.02	0.31	0.09
WALL	E4	2002	96	0.72	0.57	-0.42	0.95	1.65	0.24	0.33	0.28
WALL	E4	2003	102	0.68	0.54	-0.35	0.80	2.26	0.30	0.44	0.32
WALL	E4		799	1.10	0.48	-0.45	1.00	2.32	0.31	0.28	0.37
WALL	E7	1992	13	0.24	0.69	-0.18	0.53	0.79	0.11	0.48	0.21
WALL	E7	1994	14	0.11	0.74	-0.10	0.30	0.55	0.21	1.94	0.50
WALL	E7	1995	16	0.08	0.48	0.00	0.08	0.76	0.08	1.01	0.19
WALL	E7	1998	17	0.12	0.68	-0.01	0.26	0.93	0.35	2.89	0.57
WALL	E7	1999	16	0.18	0.57	-0.28	0.25	0.67	0.11	0.60	0.27
WALL	E7	2001	13	0.15	0.60	-0.21	0.22	0.60	0.12	0.81	0.25
WALL	E7	2003	16	0.09	0.80	-0.29	0.34	0.28	0.10	1.15	0.34
WALL	E7		132	0.75	0.59	-0.41	1.07	1.55	0.39	0.52	0.48
YP	E1	1990	508	1.56	0.48	-0.37	1.45	3.82	1.27	0.82	0.89
YP	E1	1992	799	1.05	0.36	-0.28	0.61	3.17	0.40	0.38	0.24
YP	E1	1993	684	0.55	0.44	-0.14	0.43	3.35	0.67	1.23	0.39
YP	E1	1994	1576	0.67	0.40	-0.14	0.44	3.62	0.80	1.20	0.44
YP	E1	1995	1789	0.66	0.42	-0.15	0.47	3.46	0.77	1.16	0.50
YP	E1	1996	845	0.55	0.40	-0.12	0.37	3.58	0.72	1.29	0.42
YP	E1	1997	685	0.55	0.43	-0.14	0.41	3.38	0.68	1.24	0.44
YP	E1	1998	622	1.46	0.38	-0.31	0.91	3.46	0.49	0.34	0.28
YP	E1	1999	716	1.54	0.43	-0.34	1.14	3.76	1.41	0.91	0.79
YP	E1	2000	773	1.48	0.46	-0.33	1.25	3.89	0.97	0.66	0.63
YP	E1	2001	831	1.37	0.46	-0.39	1.18	2.87	0.72	0.52	0.60
YP	E1	2002	759	2.12	0.37	-0.45	1.26	3.82	0.85	0.40	0.57
YP	E1	2003	866	2.06	0.42	-0.50	1.50	3.18	0.71	0.34	0.64
YP	E1		11453	2.00	0.35	-0.45	1.07	3.99	0.80	0.40	0.53
YP	E2	1990	282	0.22	0.50	-0.03	0.22	1.38	0.39	1.79	0.44
YP	E2	1992	1267	1.21	0.38	-0.35	0.75	3.09	0.34	0.28	0.26
YP	E2	1993	734	1.36	0.37	-0.39	0.80	3.03	0.67	0.50	0.59
YP	E2	1994	1387	0.90	0.41	-0.24	0.62	3.55	0.79	0.87	0.55
YP	E2	1995	1523	0.52	0.39	-0.01	0.34	3.51	1.00	1.93	0.55
YP	E2	1996	1404	0.45	0.37	-0.13	0.27	3.38	0.56	1.24	0.39
YP	E2	1997	1343	1.86	0.40	-0.29	1.26	4.16	1.39	0.75	0.84
YP	E2	1998	973	1.39	0.39	-0.14	0.89	4.33	0.87	0.62	0.42
YP	E2	1999	1383	3.53	0.40	-0.30	2.40	6.43	1.29	0.36	1.20
YP	E2	2000	1609	2.14	0.32	-0.39	1.03	3.69	0.53	0.25	0.39

YP	E2	2001	1657	0.72	0.47	-0.10	0.65	4.01	0.50	0.70	0.27
YP	E2	2002	1709	2.63	0.37	-0.41	1.55	4.36	0.62	0.24	0.74
YP	E2	2003	1675	2.26	0.42	-0.44	1.63	4.24	0.94	0.42	0.87
YP	E2		16964	0.79	0.29	-0.18	0.33	5.01	0.42	0.53	0.20
YP	E3	1989	1389	4.21	0.42	-0.44	3.08	7.05	1.76	0.42	1.81
YP	E3	1990	228	0.22	0.45	-0.33	0.18	0.42	0.14	0.63	0.25
YP	E3	1991	763	0.95	0.35	-0.33	0.52	2.39	0.30	0.32	0.23
YP	E3	1992	853	0.97	0.36	-0.34	0.54	2.59	0.29	0.30	0.24
YP	E3	1993	89	0.58		-0.01		1.69			
YP	E3	1994	606	0.80	0.37	-0.39	0.48	2.21	0.40	0.50	0.44
YP	E3	1995	890	0.55	0.39	-0.13	0.35	3.18	0.71	1.27	0.45
YP	E3	1997	1163	1.38	0.37	-0.37	0.82	3.70	0.74	0.53	0.53
YP	E3	1998	957	1.03	0.36	-0.18	0.58	3.83	0.55	0.53	0.30
YP	E3	1999	1718	1.41	0.34	-0.38	0.71	4.04	0.37	0.26	0.29
YP	E3	2000	1539	1.86	0.33	-0.31	0.93	4.94	0.62	0.33	0.35
YP	E3	2001	1447	1.48	0.44	-0.32	1.15	4.27	0.47	0.32	0.33
YP	E3	2002	1588	2.10	0.32	-0.44	1.01	3.53	0.44	0.21	0.41
YP	E3	2003	1391	1.94	0.35	-0.40	1.06	4.25	0.47	0.24	0.37
YP	E3		14621	2.14	0.34	-0.46	1.11	4.60	0.84	0.39	0.78
YP	E4	1989	424	1.40	0.43	-0.36	1.04	3.52	0.78	0.56	0.54
YP	E4	1990	255	0.79	0.45	-0.21	0.64	3.39	1.13	1.44	0.65
YP	E4	1991	231	0.61	0.38	-0.31	0.38	1.62	0.40	0.67	0.35
YP	E4	1992	103	0.57	0.50	-0.28	0.57	1.92	0.64	1.12	0.54
YP	E4	1993	14	0.11		0.03		1.12			
YP	E4	1994	12	0.04	0.69	-0.05	0.09	0.30	0.07	1.70	0.31
YP	E4	1995	34	0.23	0.63	0.23	0.39	1.95	0.97	4.17	0.84
YP	E4	1998	169	0.33	0.34	-0.15	0.17	2.29	0.38	1.17	0.30
YP	E4	1999	475	0.52	0.40	-0.19	0.35	2.97	0.54	1.03	0.38
YP	E4	2000	756	1.19	0.38	-0.41	0.73	2.76	0.55	0.47	0.49
YP	E4	2001	979	2.04	0.34	-0.40	1.07	3.96	0.99	0.48	0.68
YP	E4	2002	974	0.80	0.44	-0.14	0.62	4.37	0.97	1.21	0.51
YP	E4	2003	1222	1.91	0.36	-0.36	1.09	4.26	0.53	0.28	0.33
YP	E4		5648	0.98	0.32	-0.25	0.47	4.82	0.80	0.82	0.39
YP	E7	1991	58	0.39	0.82	-0.10	1.84	1.98	1.42	3.59	1.21
YP	E7	1992	15	0.48	0.76	-0.32	1.57	0.70	0.35	0.73	0.85
YP	E7	1993	64	0.36		0.05		2.10			
YP	E7	1994	59	0.39	0.46	-0.21	0.34	1.50	0.37	0.95	0.37
YP	E7	1995	133	0.25	0.45	-0.08	0.21	2.09	0.19	0.75	0.21
YP	E7	1998	226	0.61	0.43	-0.19	0.46	2.83	0.94	1.55	0.63
YP	E7	1999	238	0.35	0.45	-0.07	0.29	2.46	0.82	2.36	0.66
YP	E7	2000	342	2.06	0.41	-0.47	1.46	3.09	0.77	0.37	0.74
YP	E7	2001	352	2.76	0.48	-0.51	2.55	3.70	0.93	0.34	1.36
YP	E7	2002	434	1.55	0.52	-0.38	1.66	3.26	0.82	0.53	0.62
YP	E7	2003	280	1.02	0.35	-0.33	0.54	3.42	0.31	0.31	0.21
YP	E7		2201	1.46	0.38	-0.39	0.90	3.94	0.72	0.49	0.50

Table 6. Intrapopulation and interpopulation (years pooled) life history invariant values for lake whitefish (LWF), walleye (WALL) and yellow perch (YP) populations in Lake Ontario. Interpopulation invariants are highlighted with boxes. Maturity data were not available for these populations. Population codes correspond to Figures 1-3.

Species	Population	Year	Fish	1-BHI	2-BHI	3-BHI	Roff	Hoenig	C-B	Jensen	Mangel
LWF	O1	1992	369	0.80		-0.37		2.70			
LWF	O1	1993	439	0.92		-0.46		2.48			
LWF	O1	1994	286	0.32		-0.17		2.59			
LWF	O1	1995	343	0.64		-0.36		2.32			
LWF	O1	1996	123	0.43		-0.16		2.48			
LWF	O1	1997	120	0.25		-0.20		1.90			
LWF	O1	1998	141	0.66		-0.17		3.58			
LWF	O1	1999	94	0.69		-0.38		2.07			
LWF	O1	2000	85	0.38		-0.28		2.02			
LWF	O1	2001	123	0.94		-0.35		3.34			
LWF	O1	2002	76	0.56		-0.37		1.93			
LWF	O1	2003	58	1.06		-0.42		3.16			
LWF	O1	2004	124	1.55		-0.55		3.16			
LWF	O1		2381	1.67		-0.58		2.92			
WALL	O1	1992	455	1.15		-0.34		3.88			
WALL	O1	1993	168	0.64		-0.36		1.46			
WALL	O1	1994	167	0.89		-0.43		2.10			
WALL	O1	1995	159	0.40		-0.24		1.92			
WALL	O1	1996	328	1.28		-0.56		2.00			
WALL	O1	1997	585	0.71		-0.38		2.63			
WALL	O1	1998	494	0.64		-0.40		2.25			
WALL	O1	1999	373	1.12		-0.57		1.99			
WALL	O1	2000	220	1.18		-0.60		1.96			
WALL	O1	2001	175	1.02		-0.50		2.22			
WALL	O1	2002	272	0.87		-0.60		1.31			
WALL	O1	2003	353	2.76		-0.60		3.93			
WALL	O1	2004	392	2.31		-0.64		3.12			
WALL	O1		4141	1.61		-0.61		2.45			
YP	O1	1992	232	2.05		-0.50		3.13			
YP	O1	1993	378	1.89		-0.49		2.92			
YP	O1	1994	292	0.42		0.01		3.45			
YP	O1	1995	216	3.15		-0.58		3.73			
YP	O1	1996	208	2.35		-0.72		1.40			
YP	O1	1997	281	1.65		-0.46		2.92			
YP	O1	1998	387	1.72		-0.39		3.71			
YP	O1	1999	494	0.58		-0.17		3.27			
YP	O1	2000	519	2.34		-0.47		3.84			
YP	O1	2001	324	1.72		-0.49		2.84			
YP	O1	2002	264	1.62		-0.41		2.56			
YP	O1	2003	250	1.71		-0.43		2.95			
YP	O1	2004	393	0.88		-0.23		3.62			
YP	O1		4238	2.76		-0.50		5.00			

Table 7. Intrapopulation and interpopulation (years pooled) life history invariant values for bloater (BLO), lean lake trout (LT), lake whitefish (LWF), walleye (WALL) and yellow perch (YP) populations in Lake Huron. Interpopulation invariants are highlighted with boxes. Maturity data were not available for all of the populations. Population codes correspond to Figures 1-3.

Species	Population	Year	Fish	1-BHI	2-BHI	3-BHI	Roff	Hoenig	C-B	Jensen	Mangel
BLO	HON1	1989	1231	3.85	0.49	-0.56	3.66	5.84	0.97	0.25	1.07
BLO	HON1	1991	1028	6.19	0.48	-0.63	5.62	6.36	1.27	0.21	-1.32
BLO	HON1	1992	1141	-3.22	5.89	0.44	-0.62	4.63	5.94	1.19	0.20
BLO	HON1	2001	569	5.89	0.44	-0.62	4.63	5.94	1.19	0.20	-2.39
BLO	HON1	2002	686	3.72	0.48	-0.60	3.50	4.82	0.88	0.24	3.73
BLO	HON1	2003	986	2.88	0.49	-0.53	2.81	4.75	0.86	0.30	0.94
BLO	HON1		5642	5.38	0.40	-0.60	3.64	6.83	1.14	0.21	2.05
BLO	HON2	1986	231	-0.42	1.26	0.53	-0.38	1.43	2.54	0.73	0.58
BLO	HON2	1987	151	-1.20	1.79	0.59	-0.42	2.52	2.95	0.84	0.47
BLO	HON2	1989	1651	-2.28	5.25	0.48	-0.60	4.83	5.41	1.20	0.23
BLO	HON2	1990	319	-2.22	3.04	0.55	-0.53	3.72	4.31	0.96	0.31
BLO	HON2	1991	1341	-4.74	5.67	0.52	-0.56	6.08	7.47	1.49	0.26
BLO	HON2	1992	977	-2.76	5.66	0.67	-0.66	11.26	5.22	0.52	0.09
BLO	HON2	2001	268	-0.71	1.01	0.55	-0.40	1.24	2.75	0.50	0.49
BLO	HON2	2002	163	-0.12	0.38	0.56	-0.20	0.47	1.90	0.38	1.01
BLO	HON2	2003	437	-1.53	2.92	0.61	-0.62	4.49	3.84	1.05	0.36
BLO	HON2		5538	4.55	0.39	-0.63	2.95	5.15	0.94	0.21	-10.98
BLO	HON3	1986	441	-0.93	0.65	0.38	-0.25	0.39	3.05	0.51	0.78
BLO	HON3	1987	178	-1.62	1.79	0.52	-0.47	1.93	3.37	0.67	0.38
BLO	HON3	1988	121	-3.12	0.95	0.51	-0.14	0.98	4.62	1.15	1.21
BLO	HON3	1989	102	-1.27	2.79	0.92	-0.56	31.58	2.82	0.81	0.29
BLO	HON3	1990	84	-1.29	1.13	0.42	-0.41	0.83	2.18	0.54	0.48
BLO	HON3	1992	29	-0.33	0.18	0.67	-0.14	0.36	0.96	0.21	1.19
BLO	HON3		958	2.03	0.30	-0.50	0.88	3.66	0.61	0.30	0.38
LT	HON1	1990	1117	1.33	0.60	0.59	-0.18	0.88	1.41	1.13	1.88
LT	HON1	2003	431	-1.17	1.09	0.55	-0.24	1.32	3.45	1.54	1.41
LT	HON1		2988	1.60	0.51	-0.24	1.69	4.92	2.18	1.36	1.06
LT	HON2	1990	15	-0.22	0.23	0.93	-0.06	2.88	1.04	0.86	3.84
LT	HON2	2003	113	-0.78	0.49	0.75	-0.19	1.52	2.01	1.12	2.26
LT	HON2		140	0.70	0.75	-0.23	2.14	2.34	1.30	1.86	1.10
LWF	CORA13	2001	144	-0.77	0.41	0.64	-0.14	0.71	2.49	1.36	3.33
LWF	CORA13	2002	66	-1.33	0.78	0.72	-0.33	2.02	2.46	1.43	1.83
LWF	CORA13		210	0.89	0.68	-0.35	1.87	2.59	1.51	1.69	1.05
LWF	CORA5	1983	270	-2.48	0.94	0.67	-0.17	1.88	4.65	1.86	1.99
LWF	CORA5	1985	56	-2.77	0.33	0.64	0.02	0.58	4.33	2.17	6.51
LWF	CORA5	1986	45	-0.38	0.52	0.68	-0.28	1.11	1.50	0.66	1.27
LWF	CORA5	2000	30	-0.89	0.25	0.76	-0.06	0.79	1.98	1.39	5.49
LWF	CORA5	2001	75	-2.53	1.70	0.84	-0.35	8.68	3.76	2.93	1.72
LWF	CORA5	2002	82	-1.48	1.20	0.73	-0.42	3.27	2.86	1.32	1.11
LWF	CORA5	2003	35	-2.31	0.79	0.73	-0.24	2.12	3.01	2.11	2.67
LWF	CORA5		593	1.18	0.52	-0.27	1.26	4.94	1.90	1.61	0.84
LWF	CORA6	2000	15	-0.89	0.77	0.79	-0.40	2.90	1.45	1.13	1.47
LWF	CORA6	2001	58	-1.02	1.08	0.73	-0.46	2.96	1.91	1.22	1.13
LWF	CORA6	2002	34	-2.23	1.35	0.67	-0.41	2.76	2.90	2.11	1.57
LWF	CORA6	2003	38	-1.06	0.92	0.77	-0.40	3.04	1.84	1.10	1.20
LWF	CORA6		145	2.05	0.72	-0.46	5.38	3.57	2.27	1.11	1.65
LWF	CORA8	1985	69	-3.71	1.81	0.65	-0.32	3.31	5.16	2.34	1.30

LWF	CORA8	2001	107	-2.88	1.55	0.71	-0.32	3.70	4.23	2.54	1.64
LWF	CORA8	2002	37	-0.23	0.28	0.62	-0.26	0.46	1.04	0.57	2.03
LWF	CORA8		213	1.74	0.57	-0.35	2.33	4.27	2.33	1.34	1.11
LWF	HON1	1981	52	-1.96	0.40	0.85	0.14	2.27	3.54	2.83	7.07
LWF	HON1	1982	101	-1.28	0.28	0.71	0.08	0.68	3.11	1.56	5.63
LWF	HON1	1985	261	-0.35	0.32	0.68	-0.15	0.69	2.52	0.84	2.60
LWF	HON1	1986	158	-0.51	0.27	0.57	-0.10	0.36	2.29	0.71	2.61
LWF	HON1	1987	196	-2.45	1.12	0.73	-0.22	3.05	4.02	1.79	1.60
LWF	HON1	1988	427	-2.43	1.27	0.75	-0.25	3.90	4.04	2.24	1.76
LWF	HON1	1989	580	-3.22	1.70	0.66	-0.32	3.33	4.76	1.73	1.02
LWF	HON1	1990	767	-0.77	1.17	0.72	-0.29	2.93	3.11	1.38	1.19
LWF	HON1	1991	913	-0.64	0.72	0.61	-0.26	1.13	2.85	0.95	1.33
LWF	HON1	1992	860	-0.98	0.65	0.68	-0.18	1.40	3.61	1.51	2.33
LWF	HON1	2001	602	-0.67	1.39	0.82	-0.32	6.13	2.93	2.19	1.58
LWF	HON1	2002	487	-0.69	0.34	1.00	0.02		3.32	3.32	9.71
LWF	HON1	2003	332	-0.37	0.34	0.87	0.04	2.17	3.10	1.93	5.75
LWF	HON1		6530	0.85	0.23	-0.24	0.25	4.48	1.19	1.41	0.69
LWF	HON2	1981	131	0.66	0.39	0.85	-0.09	2.18	1.11	1.11	2.80
LWF	HON2	1982	154	-0.29	0.26	0.64	-0.03	0.47	2.34	0.94	3.58
LWF	HON2	1983	523	-0.57	1.17	0.70	-0.20	2.75	3.08	2.05	1.75
LWF	HON2	1984	338	-0.11	0.85		-0.14		2.46		
LWF	HON2	1985	626	-2.97	2.96	0.58	-0.32	4.05	5.65	2.42	0.82
LWF	HON2	1986	399	0.33	0.81	0.73	-0.21	2.24	2.06	1.37	1.70
LWF	HON2	1987	623	0.03	0.50	0.81	-0.08	2.18	2.52	1.80	3.60
LWF	HON2	1988	1414	-0.27	1.16	0.72	-0.24	2.98	3.00	1.71	1.48
LWF	HON2	1989	1238	-0.57	0.46	0.67	-0.05	0.95	3.76	1.50	3.27
LWF	HON2	1990	954	-0.64	1.11	0.68	-0.23	2.36	3.40	1.70	1.53
LWF	HON2	1991	911	-0.44	0.90	0.58	-0.24	1.24	3.32	1.33	1.48
LWF	HON2	1992	778	-0.76	1.21	0.66	-0.29	2.32	3.59	1.79	1.48
LWF	HON2	2001	216	-0.23	0.98	0.69	-0.38	2.19	1.83	1.22	1.25
LWF	HON2	2002	263	-0.24	1.06	0.75	-0.43	3.09	1.94	1.06	1.00
LWF	HON2	2003	547	0.24	0.88	0.70	-0.38	2.06	2.08	1.14	1.29
LWF	HON2		9115	2.61	0.48	-0.49	2.41	3.54	1.29	0.49	1.67
LWF	HON3	1988	96	-0.23	0.21	0.58	-0.15	0.29	1.82	0.46	2.14
LWF	HON3	1989	52	-0.63	0.24	0.66	-0.05	0.46	1.78	0.59	2.45
LWF	HON3	1990	71	-0.21	0.25	0.60	-0.10	0.37	1.97	0.49	1.99
LWF	HON3	1992	17	-0.02	0.26	0.86	-0.14	1.56	0.74	0.59	2.26
LWF	HON3	2001	83	-1.32	1.53	0.59	-0.45	2.19	2.64	0.72	0.47
LWF	HON3	2003	21	-0.47	0.13	0.85	-0.03	0.72	1.17	0.70	5.36
LWF	HON3		351	0.46	0.56	-0.23	0.60	2.71	0.68	1.46	0.50
WALL	HON1	1983	14	0.12	0.80	0.22	0.49	1.15	0.58	4.68	0.80
WALL	HON2	1984	11	-0.57	0.13	0.90	0.05	1.27	1.18	0.67	4.99
WALL	HON2	1987	18	-0.67	0.18	0.62	0.04	0.29	1.48	0.42	2.39
WALL	HON2	1988	36	-0.08	0.28	0.60	-0.15	0.43	1.22	0.30	1.09
WALL	HON2	1989	23	-0.48	1.01	0.71	-0.43	2.44	1.38	0.69	0.68
WALL	HON2	1990	25	-0.45	1.13	0.61	-0.57	1.78	1.30	0.40	0.35
WALL	HON2	1991	33	-1.28	1.09	0.66	-0.47	2.12	1.92	0.44	0.41
WALL	HON2	2001	17	-1.06	0.85	0.73	-0.34	2.26	1.79	0.80	0.94
WALL	HON2	2002	18	-0.29	0.10	0.63	-0.01	0.17	0.97	0.29	2.83
WALL	HON2	2003	19	-1.15	0.21	0.62	-0.08	0.34	1.66	0.60	2.86
WALL	HON2		208	1.29	0.47	-0.50	1.13	1.91	0.29	0.23	0.41
WALL	HON3	1998	39	1.61	0.68	-0.33	3.37	4.96	1.91	1.19	1.08
YP	HON1	1981	230	-0.92	0.37		0.03		2.94		
YP	HON1	1983	73	-2.72	0.57	0.56	0.02	0.71	4.30	1.23	2.16
YP	HON1	1985	200	0.26	0.71	0.83	-0.34	3.37	1.35	1.35	1.89
YP	HON1	1987	144	-0.85	0.33	0.52	-0.18	0.35	2.29	0.71	2.12
YP	HON1	1988	323	0.88	0.41	0.64	-0.37	0.74	0.69	0.57	1.41
YP	HON1	1989	160	-0.34	1.52		-0.47		2.08		

YP	HON1	1990	54	-0.70	0.76	0.63	-0.33	1.32	1.77	0.76	0.99
YP	HON1	1991	15	-0.20	1.00	0.53	-0.35	1.13	1.20	0.60	0.60
YP	HON1		1930	0.62	0.50	-0.20	0.61	4.00	1.23	1.99	0.71
YP	HON2	1981	13	-0.95	0.18	0.56	-0.01	0.22	1.52	0.51	2.87
YP	HON2	1982	213	-1.12	0.46	0.40	-0.08	0.31	2.79	0.35	0.75
YP	HON2	1983	204	-1.36	0.62	0.46	-0.20	0.54	2.76	0.61	0.99
YP	HON2	1984	465	-1.12	0.65	0.41	-0.20	0.45	3.18	0.64	0.98
YP	HON2	1985	755	-1.23	1.50	0.39	-0.45	0.95	2.90	1.16	0.77
YP	HON2	1986	1220	-2.19	0.59	0.41	-0.11	0.42	4.04	0.81	1.37
YP	HON2	1987	1261	-1.73	0.74	0.34	-0.18	0.39	4.34	0.39	0.53
YP	HON2	1988	971	-1.63	28.57	0.06	-0.86	1.83	3.35	0.61	0.02
YP	HON2	1989	1484	-2.47	1.18	0.30	-0.34	0.51	4.17	0.35	0.30
YP	HON2	1990	1530	-3.12	1.08	0.37	-0.28	0.62	4.70	0.78	0.73
YP	HON2	1991	994	-2.86	1.16	0.37	-0.31	0.69	4.17	0.38	0.33
YP	HON2	1992	542	-0.92	1.04	0.35	-0.33	0.57	3.12	0.31	0.30
YP	HON2	2001	47	0.23	0.65	0.51	-0.25	0.66	1.13	0.28	0.44
YP	HON2	2002	987	-1.32	0.66	0.39	-0.13	0.42	4.13	0.83	1.25
YP	HON2	2003	378	-5.35	11.96	0.39	-0.63	7.60	7.36	1.23	0.10
YP	HON2		11064	2.63	0.27	-0.52	0.96	4.48	0.37	0.14	0.30
YP	HON3	1988	13	-2.26	3.41	0.78	-0.60	11.81	3.16	1.35	0.40
YP	HON3	2001	551	-1.64	2.20	0.55	-0.34	2.64	4.03	0.00	0.00
YP	HON3	2002	193	-1.37	1.55	0.54	-0.23	1.81	3.51	2.11	1.36
YP	HON3	2003	95	-2.01	1.29	0.44	-0.31	1.02	3.16	1.35	1.05
YP	HON3		874	3.73	0.55	-0.56	4.48	4.19	0.00	0.00	0.00

* mortality estimates for interpopulation are greater than intrapopulation because the sum of young fish (age 1-3) in each age class, steepened the catch curve used to calculate mortality.

Table 8. Intrapopulation and interpopulation (years pooled) life history invariant values for bloater (BLO), lake whitefish (LWF) and yellow perch (YP) populations in Lake Michigan. Interpopulation invariants are highlighted with boxes. Maturity data were not available for all of the populations. Population codes correspond to Figures 1-3.

Species	Population	Year	Fish	1-BHI	2-BHI	3-BHI	Roff	Hoenig	C-B	Jensen	Mangel
BLO	MM1	1980	576	-2.25	1.97	0.35	-0.44	1.08	4.39	1.10	0.56
BLO	MM1	1981	351	-1.53	0.68	0.47	-0.11	0.60	3.70	1.39	2.05
BLO	MM1	1982	202	-0.11	0.14	0.51	0.00	0.14	1.21	0.54	3.97
BLO	MM1	1986	383	-2.33	0.57	0.46	0.05	0.48	4.71	2.02	3.54
BLO	MM1	1988	256	-5.22	2.78	0.73	-0.28	7.63	7.40	3.17	1.14
BLO	MM1		1768	1.63	0.32	-0.45	0.79	3.57	0.89	0.55	0.53
BLO	MM3	1980	2089	-1.19	4.31	0.32	-0.65	1.99	4.12	0.69	0.16
BLO	MM3	1981	529	-1.62	1.13	0.48	-0.11	1.05	3.87	1.55	1.36
BLO	MM3	1982	487	-2.92	0.73	0.50	0.00	0.72	5.17	2.22	3.04
BLO	MM3	1983	201	-1.98	0.74	0.40	-0.11	0.49	3.95	1.48	1.99
BLO	MM3	1985	74	-3.31	0.51		0.40		4.96		
BLO	MM3	1986	1191	0.07	0.70	0.50	-0.15	0.69	2.89	1.24	1.77
BLO	MM3	1988	582	-2.71	0.64	0.61	-0.04	1.01	5.51	1.65	2.60
BLO	MM3		5370	4.47	0.29	-0.63	1.82	4.61	1.15	0.26	1.19
BLO	MM4	1980	404	-2.64	2.85	0.33	-0.51	1.39	4.67	0.85	0.30
BLO	MM4	1981	1465	-1.02	0.56	0.32	-0.08	0.27	4.18	0.84	1.50
BLO	MM4	1982	478	-1.01	3.58	0.39	-0.40	2.30	3.42	1.71	0.48
BLO	MM4	1984	1339	-1.64	1.29	0.45	-0.18	1.05	4.16	1.39	1.08
BLO	MM4	1986	199	-1.30	0.62	0.70	-0.14	1.44	3.80	1.52	2.43
BLO	MM4		4037	3.15	0.30	-0.55	1.35	4.19	0.76	0.24	0.61
BLO	MM5	1980	100	-0.73	0.92	0.42	-0.27	0.67	2.10	0.70	0.76
BLO	MM5	1981	452	0.93	0.61	0.46	-0.34	0.51	1.27	0.54	0.89
BLO	MM5	1982	296	-1.08	1.25	0.47	-0.36	1.11	3.46	1.04	0.83
BLO	MM5	1983	143	-1.92	2.62	0.62	-0.44	4.28	3.83	1.28	0.49
BLO	MM5	1984	154	-0.51	1.33	0.53	-0.29	1.47	2.54	0.51	0.38
BLO	MM5	1985	1196	0.27	1.11	0.57	-0.15	1.49	2.74	1.37	1.23
BLO	MM5	1986	200	-3.03	1.64	0.75	-0.24	4.95	5.11	2.19	1.34
BLO	MM5		2541	1.47	0.38	-0.37	0.89	3.90	0.78	0.53	0.50
BLO	MM6		21	0.16	0.80	-0.05	0.63	1.21	0.67	4.18	0.92
LWF	CORA10	2000	114	-1.93	0.54	0.71	-0.08	1.29	3.58	2.39	4.46
LWF	CORA10	2001	218	-1.29	1.28	0.66	-0.41	2.52	3.28	1.52	1.18
LWF	CORA10	2002	148	-1.77	0.61	0.55	-0.19	0.76	3.28	1.64	2.69
LWF	CORA10	2003	51	-0.83	0.84	0.70	-0.45	2.01	1.78	0.55	0.65
LWF	CORA10		531	2.25	0.55	-0.51	2.80	3.59	1.66	0.74	1.32
LWF	CORA12	1991	51	4.22	0.66	-0.61	8.07	3.89	1.30	0.31	-0.89
LWF	CORA14	2002	31	-1.07	0.85	0.81	-0.36	3.57	2.03	1.42	1.67
LWF	CORA14	2003	21	-1.15	0.20	1.00	0.02	956.83	1.78	1.78	8.72
LWF	CORA14		52	0.94	0.81	-0.35	3.94	2.33	1.63	1.73	1.28
LWF	CORA9	2001	41	-3.72	2.21	0.82	-0.29	9.78	4.89	2.80	1.27
LWF	CORA9	2002	12	-0.52	0.11	0.94	-0.02	1.89	1.16	0.85	7.47
LWF	CORA9		58	1.46	0.82	-0.45	6.48	2.59	0.94	0.64	1.18
YP	MM1	1986	276	0.28	0.83	0.40	-0.23	0.55	1.95	0.78	0.94
YP	MM1	1996	1324	-1.34	1.39	0.55	-0.41	1.69	4.18	1.61	1.16
YP	MM1	1997	340	-0.49	2.05		-0.71		2.35		
YP	MM1	1998	257	-1.33	2.29		-0.73		3.26		
YP	MM1		2202	2.74	0.30	-0.69	1.15	4.56	0.72	0.26	0.78

YP	MM2	1980	114	-1.72	1.39	0.49	-0.20	1.34	3.62	1.45	1.04
YP	MM2	1981	106	-1.69	0.50	0.37	0.05	0.29	3.54	0.59	1.18
YP	MM2	1982	276	0.74	1.16	0.50	-0.46	1.15	1.26	0.51	0.44
YP	MM2	1983	139	-0.62	0.22	0.50	-0.05	0.22	1.44	0.72	3.33
YP	MM2		635	0.60	0.23	-0.07	0.18	3.68	0.46	0.76	0.23

Table 9. Intrapopulation and interpopulation (years pooled) life history invariant values for lake whitefish (LWF), lean lake trout (LT), siscowet lake trout (LT-SIS) and yellow perch (YP) populations in Lake Superior. Interpopulation invariants are highlighted with boxes. Maturity data were not available for all of the populations. Population codes correspond to Figures 1-3.

Species	Population	Year	Fish	1-BHI	2-BHI	3-BHI	Roff	Hoenig	C-B	Jensen	Mangel
LT	MI2	1995	82	0.70		-0.28		2.12			
LT	MI2	1996	78	2.02		-0.42		2.77			
LT	MI2	1998	96	0.88	0.84	-0.37	4.68	2.35	1.99	2.27	1.31
LT	MI2	1999	78	2.81		-0.53		2.67			
LT	MI2	2000	87	1.63		-0.28		4.56			
LT	MI2	2001	33	0.22	1.00	-0.02	1592.88*	2.25	2.25	10.04	1.60
LT	MI2	2002	72	0.53		-0.38		1.27			
LT	MI2	2003	80	0.77	0.89	-0.35	5.97	2.09	1.92	2.48	1.29
LT	MI2		606	1.44	0.81	-0.40	6.28	3.42	2.89	2.01	1.66
LT	MI3	1977	425	1.27		-0.36		2.96			
LT	MI3	1981	397	1.57	0.84	-0.44	7.95	2.61	2.61	1.66	2.14
LT	MI3	1987	39	1.11	0.82	-0.24	5.01	4.28	3.50	3.15	1.38
LT	MI3	1995	63	0.37		-0.27		1.55			
LT	MI3	1996	87	0.55	1.00	-0.17	3648.47*	2.96	2.42	4.41	1.51
LT	MI3	1998	121	1.15		-0.50		2.23			
LT	MI3	1999	105	1.77	0.72	-0.61	4.45	2.14	2.14	1.21	1.52
LT	MI3	2000	114	0.50	1.00	-0.37	3439.39*	2.06	1.75	3.51	1.54
LT	MI3	2001	96	0.84	0.97	-0.30	28.57	2.61	2.13	2.54	1.31
LT	MI3	2002	110	1.12		-0.29		3.36			
LT	MI3	2003	89	0.18	1.00	-0.22	1634.83*	1.59	1.59	8.85	1.96
LT	MI3		1672	1.68	0.75	-0.49	5.12	4.44	3.14	1.87	1.84
LT	MI4	1971	141	0.98	0.73	-0.26	2.68	3.11	2.80	2.85	1.42
LT	MI4	1972	151	2.84	0.79	-0.50	10.80	3.40	1.86	0.65	-2.94
LT	MI4	1975	111	2.62	0.78	-0.43	9.16	4.40	3.60	1.37	2.88
LT	MI4	1977	529	3.93	0.70	-0.44	9.18	7.27	5.04	1.28	3.83
LT	MI4	1980	220	3.89	0.67	-0.41	8.08	7.83	4.82	1.24	2.57
LT	MI4	1981	198	1.37	0.71	-0.26	3.40	5.92	3.38	2.47	1.23
LT	MI4	1982	119	0.77	0.67	-0.18	1.54	5.46	2.73	3.57	0.91
LT	MI4	1983	427	1.25	0.54	-0.38	1.46	3.24	1.73	1.38	0.94
LT	MI4	1987	82	0.29	0.76	0.00	0.95	3.49	2.62	8.91	1.13
LT	MI4	1995	257	0.77		-0.11		4.85			
LT	MI4	1996	328	2.34	0.92	-0.47	27.30	4.16	3.52	1.51	2.34
LT	MI4	1997	366	1.44	0.79	-0.45	5.43	3.29	2.90	2.02	1.97
LT	MI4	1998	360	1.56	0.96	-0.52	33.41	2.98	2.45	1.57	1.90
LT	MI4	1999	322	1.90		-0.51		3.31			
LT	MI4	2000	445	0.60	1.00	-0.22	4424.32*	3.79	3.79	6.30	1.96
LT	MI4	2001	417	2.96	0.90	-0.42	26.46	5.19	5.19	1.76	3.75
LT	MI4	2002	279	2.03	0.83	-0.41	9.99	4.19	4.19	2.06	2.23
LT	MI4	2003	215	2.19		-0.52		2.64			
LT	MI4		4967	2.69	0.56	-0.51	3.45	4.40	2.33	0.86	1.51
LT	MI5	1975	16	0.11	0.71	0.05	0.27	1.64	0.82	7.40	0.70
LT	MI5	1980	200	1.56	0.57	-0.34	2.05	4.99	2.33	1.49	1.01
LT	MI5	1981	198	1.21	0.59	-0.37	1.76	3.00	1.38	1.15	0.84
LT	MI5	1982	239	1.23	0.61	-0.43	1.88	2.98	1.23	1.00	0.93
LT	MI5	1983	265	0.67	0.60	-0.21	1.02	3.82	2.04	3.04	0.87
LT	MI5	1987	50	0.31	0.77	-0.01	1.03	3.51	2.64	8.60	1.05
LT	MI5	1995	180	0.33	1.00	-0.09	2402.44*	2.87	2.87	8.73	1.69
LT	MI5	1996	200	1.01	0.99	-0.31	82.83	3.32	3.04	3.01	1.73
LT	MI5	1998	247	1.34	0.92	-0.43	15.62	2.86	2.86	2.13	2.11
LT	MI5	1999	277	0.86	0.59	-0.32	1.23	3.30	2.42	2.83	1.37
LT	MI5	2000	206	0.35	1.00	-0.27	3192.69*	2.47	2.47	6.99	1.87
LT	MI5	2001	178	0.67	1.00	-0.21	5049.69*	3.27	3.00	4.45	1.57
LT	MI5	2002	181	0.37	0.82	-0.23	1.69	2.71	1.42	3.84	1.02
LT	MI5	2003	195	1.33	0.80	-0.44	5.16	2.90	1.93	1.46	1.34

LT	MI5		2653	1.58	0.60	-0.47	2.35	4.30	1.61	1.02	0.99
LT	MI6	1975	50	1.07	0.77	-0.32	3.66	3.45	1.86	1.73	1.20
LT	MI6	1980	121	1.02	0.62	-0.37	1.68	2.55	1.57	1.54	0.98
LT	MI6	1981	136	0.87	0.88	-0.23	6.49	3.26	2.93	3.39	1.40
LT	MI6	1982	136	1.10	0.67	-0.38	2.19	2.99	1.60	1.45	0.94
LT	MI6	1983	314	1.63	0.68	-0.35	3.41	4.15	3.46	2.12	1.54
LT	MI6	1987	34	0.22	0.91	0.00	2.32	2.43	1.99	9.12	1.13
LT	MI6	1995	42	0.34		0.04		3.59			
LT	MI6	1996	51	1.42	0.85	-0.37	7.88	2.86	2.57	1.81	1.41
LT	MI6	1997	224	1.07	0.74	-0.44	2.98	2.95	1.92	1.79	1.35
LT	MI6	1998	54	2.02		-0.49		2.52			
LT	MI6	1999	169	1.39	0.80	-0.56	5.67	2.40	1.39	1.00	1.47
LT	MI6	2000	151	0.55	0.73	-0.23	1.50	3.04	2.23	4.08	1.27
LT	MI6	2001	46	1.74	0.94	-0.30	27.55	5.00	5.00	2.88	2.38
LT	MI6	2002	79	0.39	0.98	-0.32	24.57	1.74	1.36	3.51	1.41
LT	MI6	2003	72	0.37		-0.01		3.50			
LT	MI6		1679	2.61	0.54	-0.55	3.02	4.33	2.16	0.83	2.03
LT	MI7	1981	222	1.21	0.76	-0.38	3.78	2.94	1.81	1.50	1.16
LT	MI7	1983	171	2.11	0.70	-0.45	5.00	3.97	2.84	1.34	1.69
LT	MI7	1987	26	0.62	0.84	-0.17	3.31	3.34	2.43	3.91	0.98
LT	MI7	1995	317	2.00	0.78	-0.52	7.08	3.20	2.35	1.17	2.22
LT	MI7	1996	54	2.05		-0.28		5.85			
LT	MI7	1997	179	1.44	0.65	-0.48	2.61	2.80	1.57	1.10	1.36
LT	MI7	1998	188	1.65	0.73	-0.47	4.40	3.27	1.96	1.19	1.57
LT	MI7	1999	289	1.89	0.46	-0.55	1.61	2.98	1.32	0.70	1.15
LT	MI7	2000	348	2.38	0.68	-0.73	5.08	2.58	0.99	0.42	293.84
LT	MI7	2001	187	1.13	0.66	-0.33	2.20	4.01	2.41	2.13	1.42
LT	MI7	2002	199	1.12	0.72	-0.33	2.88	3.76	2.41	2.15	1.22
LT	MI7	2003	162	2.85	0.69	-0.55	6.45	3.85	2.57	0.90	2.00
LT	MI7		2354	5.15	0.66	-0.76	9.95	4.35	0.33	0.07	-0.23
LT	MI8	1975	66	0.26	0.86	0.01	1.52	3.24	2.16	8.40	1.04
LT	MI8	1981	49	0.33	0.68	-0.06	0.71	2.76	1.76	5.30	1.02
LT	MI8	1982	108	1.21	0.81	-0.41	5.33	2.34	1.95	1.61	1.47
LT	MI8		223	1.61	0.81	-0.39	7.08	3.37	2.80	1.74	1.76
LT	SON1	1988	2176	4.01		-0.49		6.34			
LT	SON1	1989	1806	2.23		-0.40		5.71			
LT	SON1	1990	1590	4.64		-0.57		4.80			
LT	SON1	1991	2106	3.20		-0.46		5.67			
LT	SON1	1992	366	1.57		-0.48		4.46			
LT	SON1	1993	529	1.16		-0.39		4.89			
LT	SON1	1994	492	2.88		-0.66		4.30			
LT	SON1	1995	1361	16.25		-1.04		4.28			
LT	SON1		10429	7.07		-0.84		4.63			
LT	WI1	1987	633	2.24		-0.52		3.46			
LT	WI1	1988	208	0.85		-0.29		3.70			
LT	WI1	1989	344	0.56		-0.25		3.17			
LT	WI1	1990	264	0.67		-0.24		4.14			
LT	WI1	1991	338	1.14		-0.39		3.14			
LT	WI1	1992	220	0.48		-0.23		3.19			
LT	WI1	1993	443	1.08		-0.44		2.70			
LT	WI1	1994	197	0.59		-0.27		2.81			
LT	WI1	1995	335	0.82		-0.41		2.31			
LT	WI1	1997	92	0.79		-0.39		2.30			
LT	WI1	1998	132	0.89		-0.32		3.49			
LT	WI1	1999	196	0.45		-0.23		2.67			
LT	WI1	2000	125	0.47		-0.25		2.61			
LT	WI1	2002	67	0.30		-0.27		1.90			
LT	WI1		3619	1.09		-0.35		4.70			
LT	WI2	1981	384	1.06		-0.29		3.99			

LT	WI2	1982	251	0.83		-0.25		3.58			
LT	WI2	1983	121	1.09		-0.24		4.22			
LT	WI2	1984	178	0.44		-0.18		3.18			
LT	WI2	1985	1153	3.24		-0.45		6.27			
LT	WI2	1986	1975	2.61		-0.52		4.60			
LT	WI2	1987	1543	1.93		-0.45		3.71			
LT	WI2	1988	1063	1.48		-0.44		3.87			
LT	WI2	1989	1374	2.77		-0.51		4.57			
LT	WI2	1990	783	2.32		-0.57		3.80			
LT	WI2	1991	867	1.72		-0.47		3.78			
LT	WI2	1992	560	1.44		-0.45		3.43			
LT	WI2	1993	426	1.10		-0.39		3.82			
LT	WI2	1994	530	0.87		-0.39		3.47			
LT	WI2	1995	387	1.54		-0.49		2.93			
LT	WI2	1997	511	0.61		-0.37		3.04			
LT	WI2	1998	442	0.77		-0.43		2.94			
LT	WI2	1999	499	0.63		-0.33		3.21			
LT	WI2	2000	705	0.69		-0.35		3.55			
LT	WI2	2002	161	0.40		-0.37		2.28			
LT	WI2	2003	56	0.36	0.60	-0.11	0.54	3.27	1.31	3.66	0.60
LT	WI2		13967	2.93		-0.61		5.46			
LWF	MI2	1995	23	0.27	0.92	-0.09	2.90	1.12	1.12	4.19	1.08
LWF	MI2		40	0.18	0.75	-0.09	0.54	1.59	0.73	4.11	0.77
LWF	MI3	1995	184	1.56	0.64	-0.38	2.73	2.86	2.23	1.43	1.18
LWF	MI3	1998	70	0.31	0.74	-0.12	0.88	2.32	1.35	4.35	0.93
LWF	MI3	2003	110	0.60	0.91	-0.35	5.90	2.01	1.23	2.05	1.09
LWF	MI3		364	1.75	0.64	-0.48	3.07	3.13	1.69	0.96	1.19
LWF	MI4	1998	13	0.83		0.05		6.00			
LWF	MI4		13	0.83		0.05		6.00			
LWF	MI5	2002	17	0.64	0.87	-0.33	4.46	1.73	0.86	1.35	1.09
LWF	MI5		21	0.71	0.81	-0.32	3.04	1.97	1.18	1.67	1.26
LWF	MI6	1995	19	0.22	1.00	0.12	1104.90*	2.49	2.49	11.10	1.43
LWF	MI6	1998	94	1.60		-0.39		3.06			
LWF	MI6	2002	25	0.25	0.54	-0.09	0.30	1.72	0.69	2.72	0.65
LWF	MI6	2003	61	0.38	1.00	-0.14	1796.46*	2.17	1.95	5.18	1.60
LWF	MI6		199	2.80		-0.55		2.80			
LWF	MI7	1981	178	0.88	0.60	-0.34	1.30	2.77	0.79	0.90	0.60
LWF	MI7	1982	431	1.40	0.60	-0.44	2.08	3.32	0.83	0.59	0.74
LWF	MI7	1983	403	0.76	0.72	-0.22	1.92	4.05	1.16	1.52	0.70
LWF	MI7	1984	417	1.60	0.67	-0.38	3.26	4.51	1.29	0.81	1.23
LWF	MI7	2001	79	0.21	0.65	-0.10	0.40	1.80	0.69	3.24	0.73
LWF	MI7	2002	99	1.33	0.59	-0.40	1.88	2.19	1.22	0.91	0.94
LWF	MI7	2003	55	0.31	0.61	-0.13	0.47	1.95	0.89	2.89	0.75
LWF	MI7		1662	1.81	0.49	-0.44	1.76	4.27	1.34	0.74	0.97
LWF	MI8	2001	57	1.77	0.73	-0.38	4.90	2.96	1.85	1.04	1.58
LWF	MI8	2002	13	0.16		-0.17		0.42			
LWF	MI8		79	1.04	0.69	-0.38	2.35	1.76	1.32	1.27	1.18
LWF	WI2	1991	19	0.22		-0.05		2.17			
LWF	WI2		41	0.67		-0.42		1.43			
LWF	SON1	1989	2372	3.46		-0.52		5.69			
LWF	SON1	1991	1989	3.34		-0.53		5.50			
LWF	SON1	1992	5351	2.97		-0.48		7.07			
LWF	SON1	1993	4421	9.05		-0.70		6.35			
LWF	SON1	1994	3872	5.34		-0.58		6.70			
LWF	SON1	1995	4042	12.40		-0.68		10.99			
LWF	SON1	1996	1372	3.31		-0.66		3.55			

LWF	SON1		23419	4.61		-0.61		6.12			
LT-SIS	MI2	1995	20	0.30	1.00	-0.18	1935.21*	2.36	2.36	7.97	1.49
LT-SIS	MI2	1996	82	0.65	0.73	-0.46	1.73	1.91	1.39	2.13	1.02
LT-SIS	MI2	1998	48	0.51	0.74	-0.28	1.49	3.44	2.39	4.68	1.09
LT-SIS	MI2	1999	42	0.47	0.82	-0.29	2.10	2.59	1.91	4.03	1.09
LT-SIS	MI2	2000	66	0.37	0.85	-0.39	2.00	1.73	1.38	3.77	1.15
LT-SIS	MI2	2001	67	1.94	0.77	-0.57	6.47	3.53	3.19	1.65	1.84
LT-SIS	MI2	2002	52	0.19	0.72	-0.32	0.48	1.36	0.89	4.67	0.99
LT-SIS	MI2	2003	105	2.55	0.76	-0.62	7.96	4.39	3.16	1.24	2.20
LT-SIS	MI2		482	0.64	0.68	-0.44	1.36	2.69	1.76	2.74	1.11
LT-SIS	MI3	1995	213	1.20	0.69	-0.51	2.73	2.38	1.96	1.63	1.33
LT-SIS	MI3	1996	418	2.53	0.69	-0.56	5.65	4.28	3.38	1.34	1.89
LT-SIS	MI3	1998	216	0.46	0.71	-0.36	1.10	2.58	1.68	3.67	1.08
LT-SIS	MI3	1999	163	0.51	0.78	-0.35	1.78	2.63	1.86	3.62	1.07
LT-SIS	MI3	2000	164	0.81	0.88	-0.49	5.85	2.43	1.93	2.37	1.30
LT-SIS	MI3	2001	201	1.05	0.80	-0.51	4.24	2.59	2.23	2.13	1.45
LT-SIS	MI3	2002	184	2.05	0.72	-0.55	5.28	4.65	3.72	1.81	1.92
LT-SIS	MI3	2003	183	0.45	0.74	-0.46	1.28	1.70	1.15	2.56	0.99
LT-SIS	MI3		1742	1.39	0.71	-0.55	3.49	3.54	2.40	1.72	1.40
LT-SIS	MI4	1995	205	3.78	0.66	-0.64	7.44	4.85	3.15	0.83	2.90
LT-SIS	MI4	1996	362	1.96	0.66	-0.54	3.85	4.47	2.80	1.43	1.65
LT-SIS	MI4	1997	271	1.54	0.71	-0.50	3.81	4.47	3.04	1.97	2.13
LT-SIS	MI4	1998	227	3.52	0.76	-0.59	10.95	6.02	4.65	1.32	2.20
LT-SIS	MI4	1999	285	1.68	0.69	-0.60	3.67	2.65	2.17	1.29	1.33
LT-SIS	MI4	2000	172	0.86	0.78	-0.57	3.10	1.73	1.15	1.33	0.88
LT-SIS	MI4	2001	214	0.70	0.79	-0.45	2.67	2.19	1.79	2.58	1.17
LT-SIS	MI4	2002	234	0.65	0.73	-0.56	1.74	1.43	1.09	1.68	0.96
LT-SIS	MI4	2003	201	0.77	0.74	-0.59	2.25	1.47	1.23	1.59	1.04
LT-SIS	MI4		2171	1.34	0.59	-0.58	1.96	2.61	1.77	1.32	1.19
LT-SIS	MI5	1995	122	3.02	0.74	-0.55	8.69	4.82	4.25	1.41	2.35
LT-SIS	MI5	1996	206	4.53	0.65	-0.56	8.39	7.14	5.95	1.31	3.03
LT-SIS	MI5	1997	502	1.70	0.67	-0.46	3.45	5.85	3.51	2.07	1.49
LT-SIS	MI5	1998	189	6.93	0.55	-0.73	8.59	5.57	3.88	0.56	4.30
LT-SIS	MI5	1999	159	2.73	0.72	-0.61	7.19	4.37	3.04	1.12	1.90
LT-SIS	MI5	2000	164	2.12	0.93	-0.54	28.39	5.00	4.32	2.04	2.70
LT-SIS	MI5	2001	141	1.15	0.79	-0.56	4.30	2.29	1.56	1.36	1.13
LT-SIS	MI5	2002	161	5.18	0.64	-0.57	9.13	9.30	6.76	1.30	2.65
LT-SIS	MI5	2003	192	0.90	0.72	-0.41	2.29	3.99	2.76	3.05	1.24
LT-SIS	MI5		1836	3.37	0.49	-0.69	3.18	3.65	2.25	0.67	1.45
LT-SIS	MI6	1980	13	0.28	0.74	-0.03	0.81	2.62	1.43	5.18	0.76
LT-SIS	MI6	1995	88	2.61	0.86	-0.52	16.30	4.50	3.94	1.51	2.79
LT-SIS	MI6	1996	141	1.84	0.83	-0.54	9.10	3.77	2.82	1.54	2.20
LT-SIS	MI6	1998	124	0.76	0.98	-0.55	29.93	1.79	1.42	1.87	1.18
LT-SIS	MI6	1999	78	1.22	0.72	-0.52	3.07	3.08	2.10	1.72	1.44
LT-SIS	MI6	2000	111	0.47	0.69	-0.50	1.05	1.53	1.09	2.34	0.97
LT-SIS	MI6	2001	153	0.98	0.82	-0.40	4.46	3.42	2.88	2.95	1.67
LT-SIS	MI6	2002	137	1.21	0.81	-0.58	5.17	2.36	1.95	1.60	1.62
LT-SIS	MI6	2003	112	0.47	0.99	-0.35	32.11	2.62	1.99	4.24	1.44
LT-SIS	MI6		963	1.71	0.65	-0.60	3.21	3.52	2.26	1.32	1.66
LT-SIS	MI7	1995	59	0.64	0.89	-0.76	5.35	0.75	0.32	0.50	0.67
LT-SIS	MI7	1996	82	2.93	0.67	-0.89	6.04	1.50	1.44	0.49	-4.82
LT-SIS	MI7	1997	181	5.04	0.75	-0.93	14.95	2.72	1.17	0.23	-0.27
LT-SIS	MI7	1998	226	2.27	0.73	-0.83	6.23	2.08	0.94	0.41	-4.22
LT-SIS	MI7	1999	87	0.32	0.88	-0.34	2.31	1.62	1.16	3.67	1.08
LT-SIS	MI7	2000	22	0.14	0.72	-0.25	0.37	0.96	0.53	3.70	0.72
LT-SIS	MI7	2001	142	1.10	0.67	-0.48	2.26	2.75	1.30	1.18	1.09
LT-SIS	MI7	2002	86	1.14	0.61	-0.65	1.79	1.73	0.73	0.65	0.73
LT-SIS	MI7	2003	67	0.52	0.78	-0.55	1.86	1.61	0.57	1.10	0.93
LT-SIS	MI7	2004	12	0.16	0.65	-0.38	0.31	0.62	0.33	2.00	0.49

LT-SIS	MI7		964	4.12	0.61	-0.86	6.38	3.00	1.16	0.28	-1.06
YP	SON1	1991	219	3.11		-0.47		3.80			
YP	SON1	1992	241	3.54		-0.61		3.92			
YP	SON1	1993	252	1.33		-0.39		3.53			
YP	SON1	1994	288	2.13		-0.52		3.44			
YP	SON1	1995	433	12.21		-0.80		4.78			
YP	SON1	1996	157	4.75		-0.84		2.42			
YP	SON1		1590	2.80		-0.55		4.02			

*Denote abnormal Roff values that occurred when the L_r and lengths at maturity (L_α) were similar. These results indicate that the populations were under sampled in those years.

Table 10. Life history invariant values of cohorts used in the virtual population analyses. Population codes correspond to Figures 1-3. The last two digits in the population code represent the start of each cohort for e.g. EWAL1C90 = Walleye population 1 from Lake Erie, cohort start 1990. Age represents the ages with data for each cohort.

Species	Population	Age	1-BHI	2-BHI	3-BHI	Roff	Hoenig	C-B	Jensen	Mangel
WALL	EWAL1C90	0, 2-9, 11	1.21	0.44	-0.39	0.96	2.45	0.45	0.37	0.38
WALL	EWAL1C91	1-7, 9	0.40	0.54	-0.12	0.47	2.81	0.70	1.77	0.52
WALL	EWAL1C92	0-8, 10-11	0.69	0.56	-0.40	0.89	1.42	0.26	0.37	0.35
WALL	EWAL2C89	1, 3-9, 11	0.36	0.56	-0.13	0.47	2.31	0.63	1.73	0.53
WALL	EWAL2C90	0-8, 10, 13	0.53	0.51	-0.19	0.56	3.01	0.46	0.87	0.42
WALL	EWAL2C91	1-6, 8-9	0.97	0.42	-0.31	0.69	2.37	0.53	0.54	0.48
YP	EYP1C91	2-9	1.25	0.37	-0.33	0.73	3.11	0.39	0.31	0.27
YP	EYP1C92	2-9	1.34	0.46	-0.36	1.15	3.09	0.77	0.58	0.64
YP	EYP1C93	2-9	1.57	0.42	-0.39	1.14	3.53	0.79	0.50	0.56
YP	EYP2C91	1-6	1.56	0.44	-0.31	1.25	3.23	0.54	0.35	0.48
YP	EYP2C93	1-5, 7-8	1.29	0.38	-0.30	0.79	3.53	0.88	0.68	0.58
YP	HYPON2C81	1-10	0.67	0.39	-0.15	0.42	3.88	0.39	0.58	0.20
YP	OYP1C91	1-8	1.85		-0.44		3.43			
YP	OYP1C92	1-8	1.48		-0.42		2.89			
YP	OYP1C94	1-7	2.04		-0.53		2.53			
LWF	HLWFON2C80	1-6	0.68	0.81	-0.04	2.91	4.03	2.88	4.21	1.46
LWF	HLWFON2C81	1-7, 10	0.68	0.64	-0.21	1.23	2.86	1.14	1.69	0.85
LWF	HLWFON2C82	1-8, 10	0.44	0.56	-0.09	0.55	3.06	0.92	2.11	0.66
LWF	OLWF1C91	1-13	0.79		-0.50		1.28			
LWF	OLWF1C92	0-12	0.56		-0.43		1.16			
LWF	OLWF1C93	1-11	0.24		-0.38		0.57			
LWF	OLWF1C94	1-10	0.91		-0.44		1.45			
LT-SIS	SLTSISMI7C92	3-11	2.36	0.73	-0.49	6.48	3.41	2.79	1.18	2.63
LT	SLTWI2C85	1-10	0.90		-0.37		1.84			

Figure 1. Extent of (a) 12 lean lake trout and (b) 6 siscowet lake trout populations used to examine life history traits in the Great Lakes basin. Black lines delineate population zones.

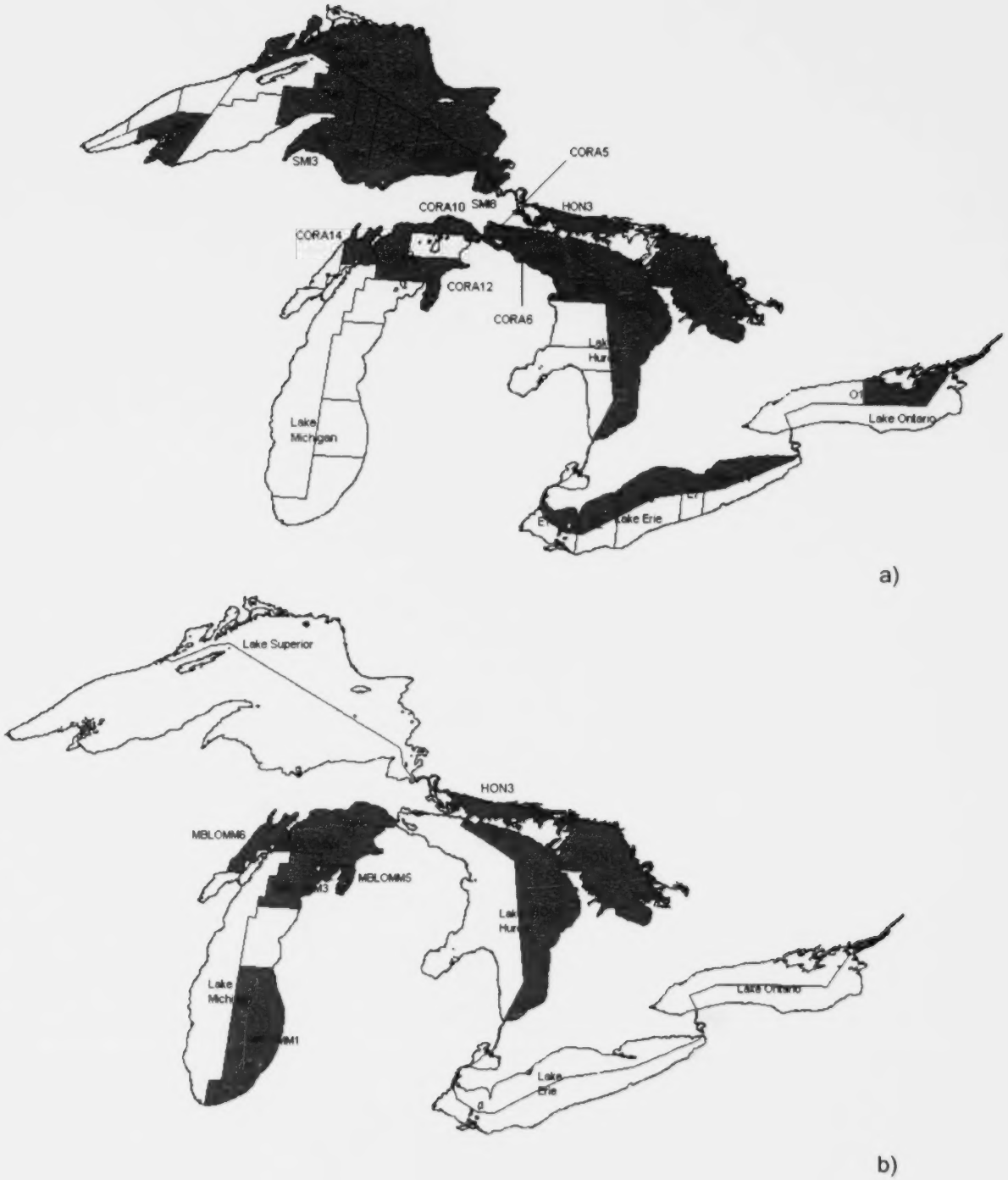

Figure 2. Extent of (a) 26 lake whitefish and (b) 8 bloater populations used to examine life history traits in the Great Lakes basin. Black lines delineate population zones.

Figure 1. Extent of (a) 12 lean lake trout and (b) 6 siscowet lake trout populations used to examine life history traits in the Great Lakes basin. Black lines delineate population zones.

Figure 2. Extent of (a) 26 lake whitefish and (b) 8 bloater populations used to examine life history traits in the Great Lakes basin. Black lines delineate population zones.

Figure 3. Extent of (a) 12 yellow perch and (b) 9 walleye populations used to examine life history traits in the Great Lakes basin. Black lines delineate population zones.

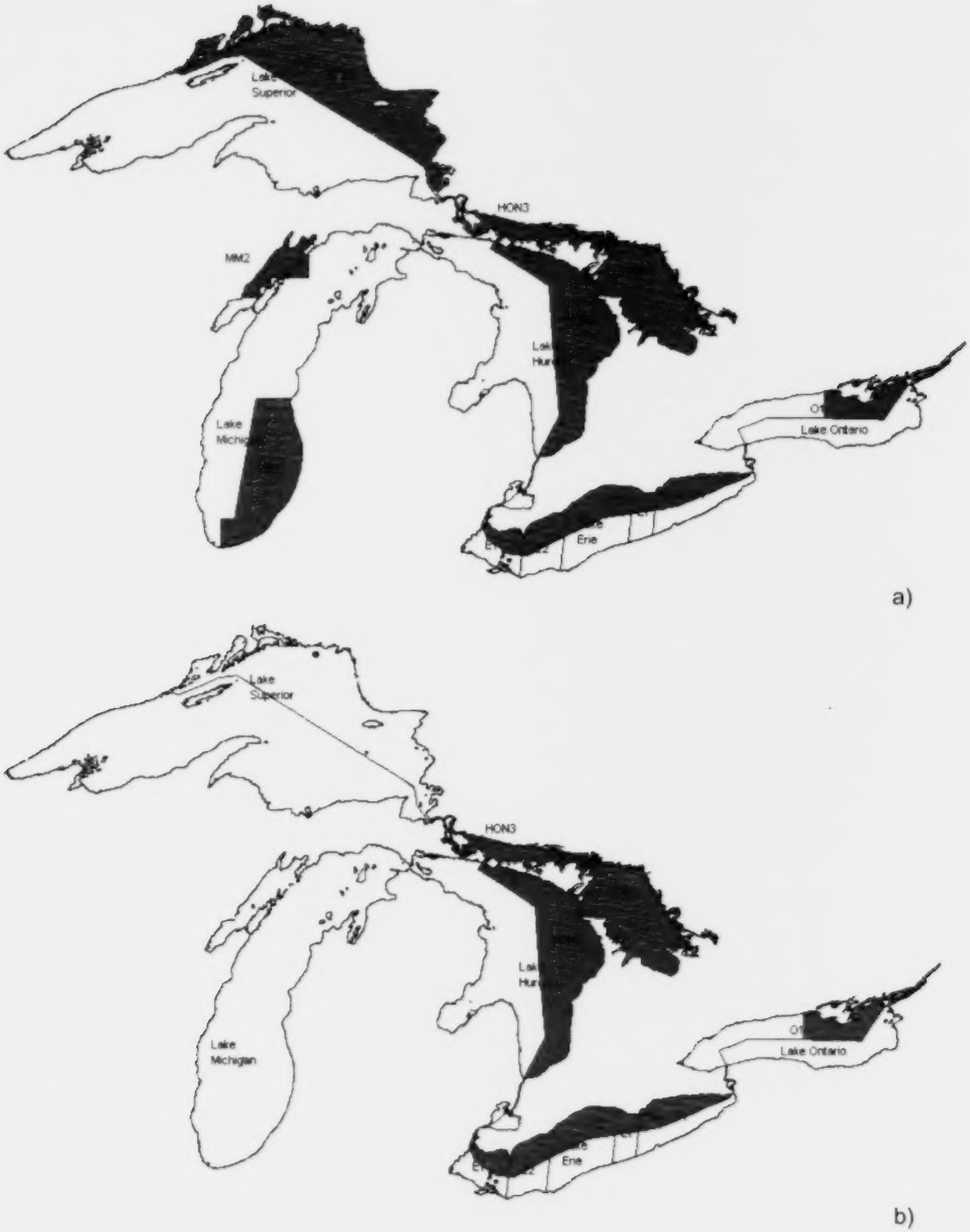

Figure 3. Extent of (a) 12 yellow perch and (b) 9 walleye populations used to examine life history traits in the Great Lakes basin. Black lines delineate population zones.

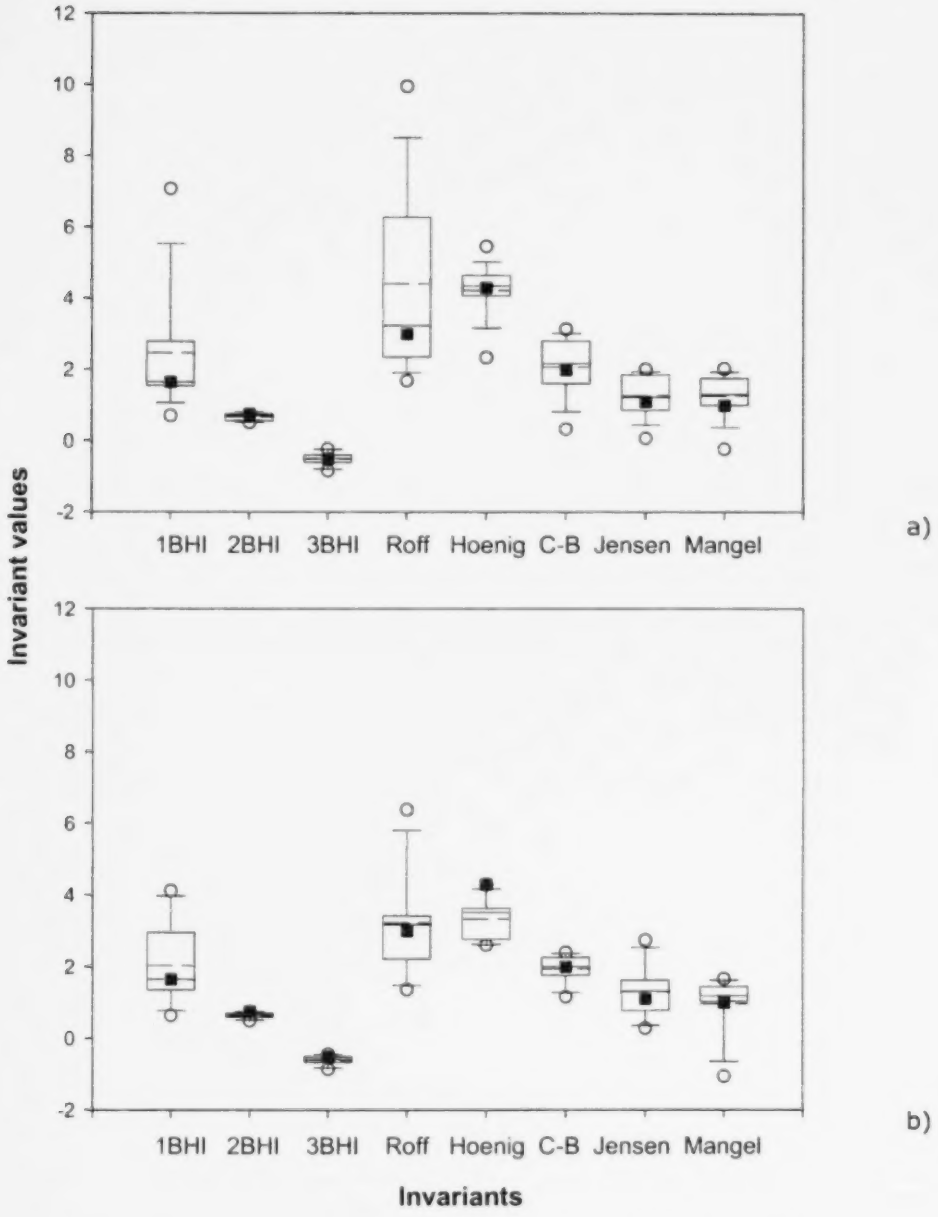

Figure 4. Mean (dashed lines) invariant values for a) lake trout and b) siscowet lake trout populations in the Great Lakes. Solid horizontal lines represent median values, boxes represent the 25th and 75th percentiles, whiskers represent the 10th and 90th percentiles and black squares represent the proposed invariant value for each of the invariants. Open circles indicate outliers.

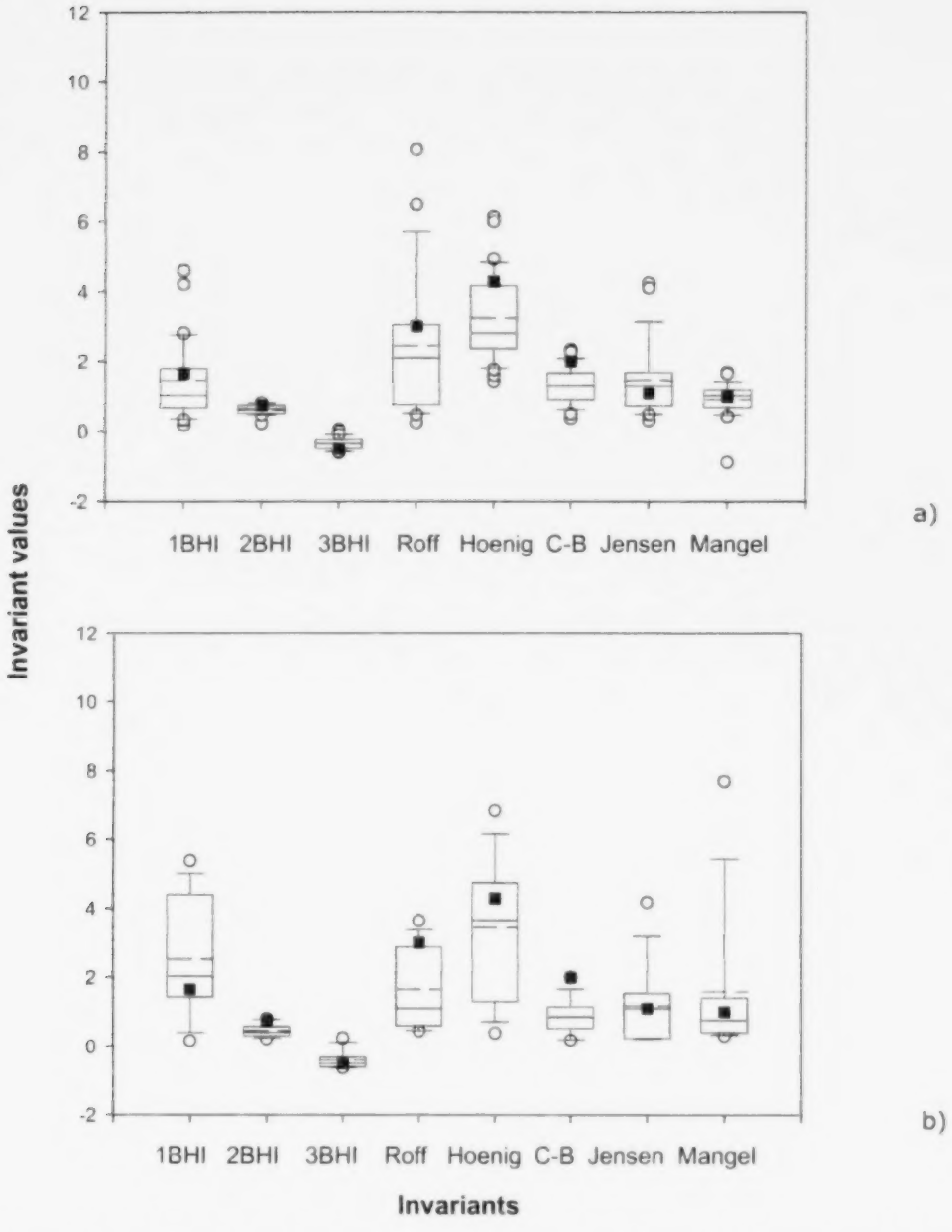

Figure 5. Mean (dashed lines) invariant values for a) lake whitefish and b) bloater populations in the Great Lakes. Solid horizontal lines represent median values, boxes represent the 25th and 75th percentiles, whiskers represent the 10th and 90th percentiles and black squares represent the proposed invariant value for each of the invariants. Open circles indicate outliers.

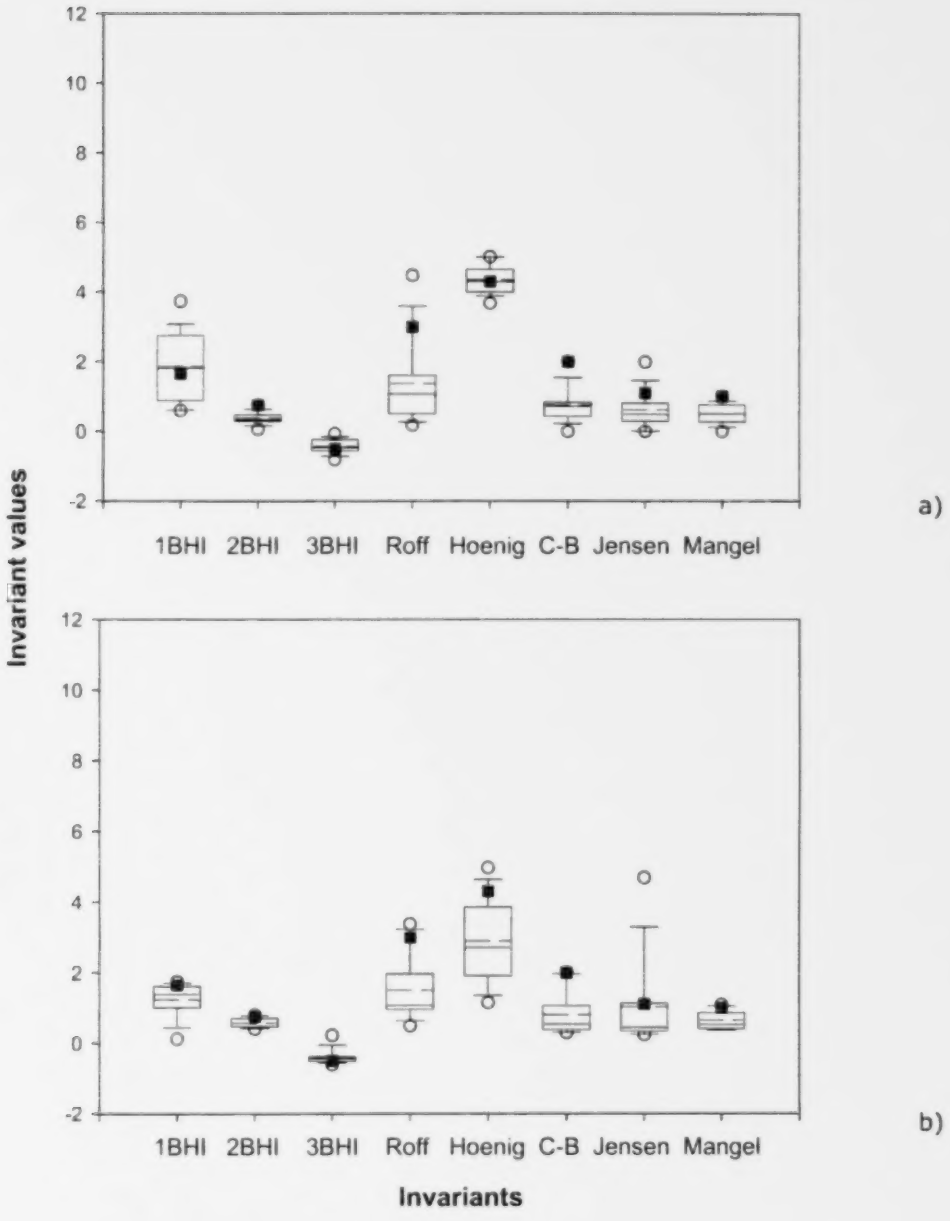

Figure 6. Mean (dashed lines) invariant values for a) yellow perch and b) walleye populations in the Great Lakes. Solid horizontal lines represent median values, boxes represent the 25th and 75th percentiles, whiskers represent the 10th and 90th percentiles and black squares represent the proposed invariant value for each of the invariants. Open circles indicate outliers.

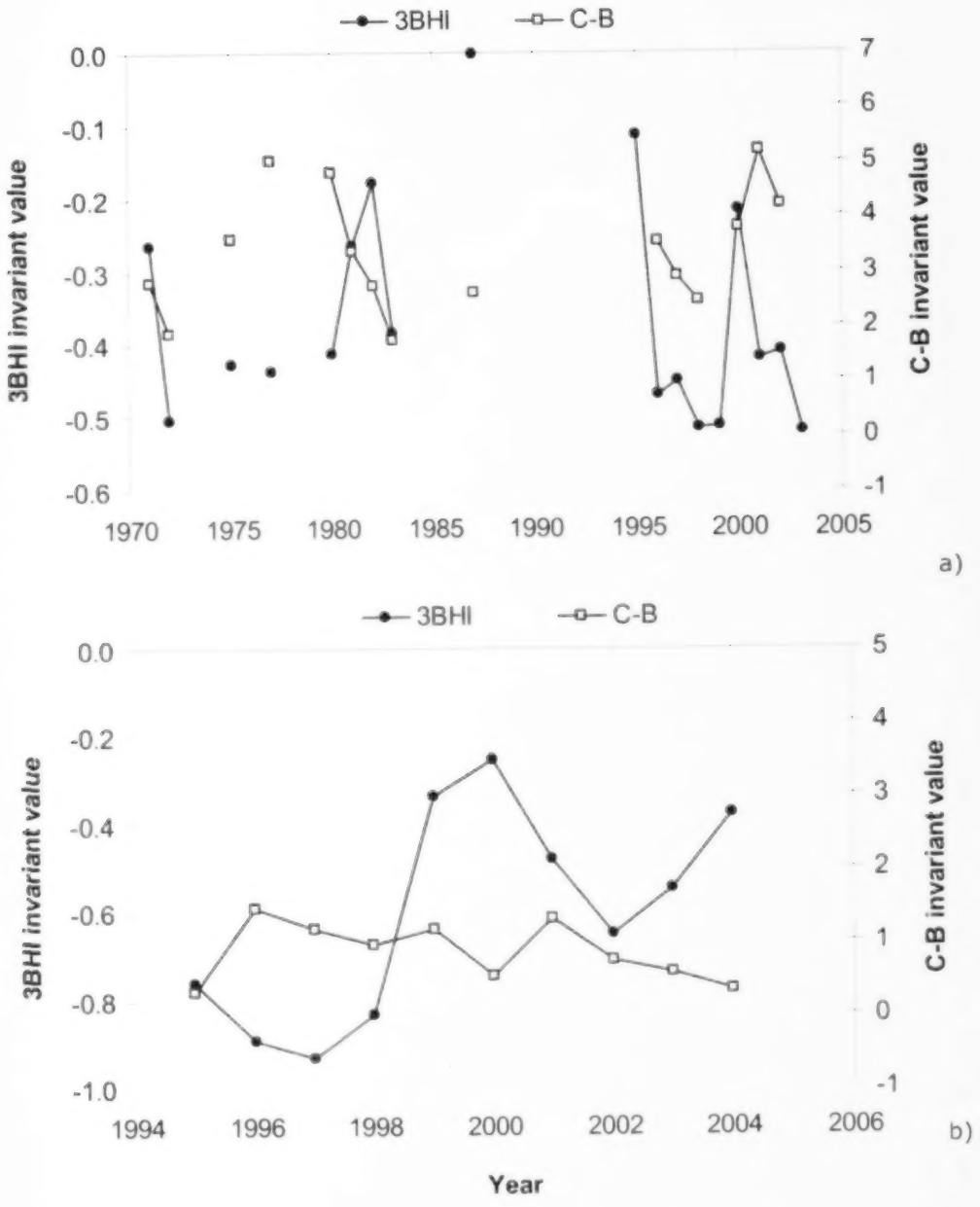

Figure 7. Intrapopulation changes in the 3rd Beverton-Holt (3BHI) and Charnov-Berrigan (C-B) invariants through time for a) lean lake trout in Lake Superior and b) siscowet lake trout in Lake Superior, population codes are SLTMI4 and SLTSISMI7, respectively. Proposed invariant values are -0.5 for the 3BHI and 2 for the C-B invariant.

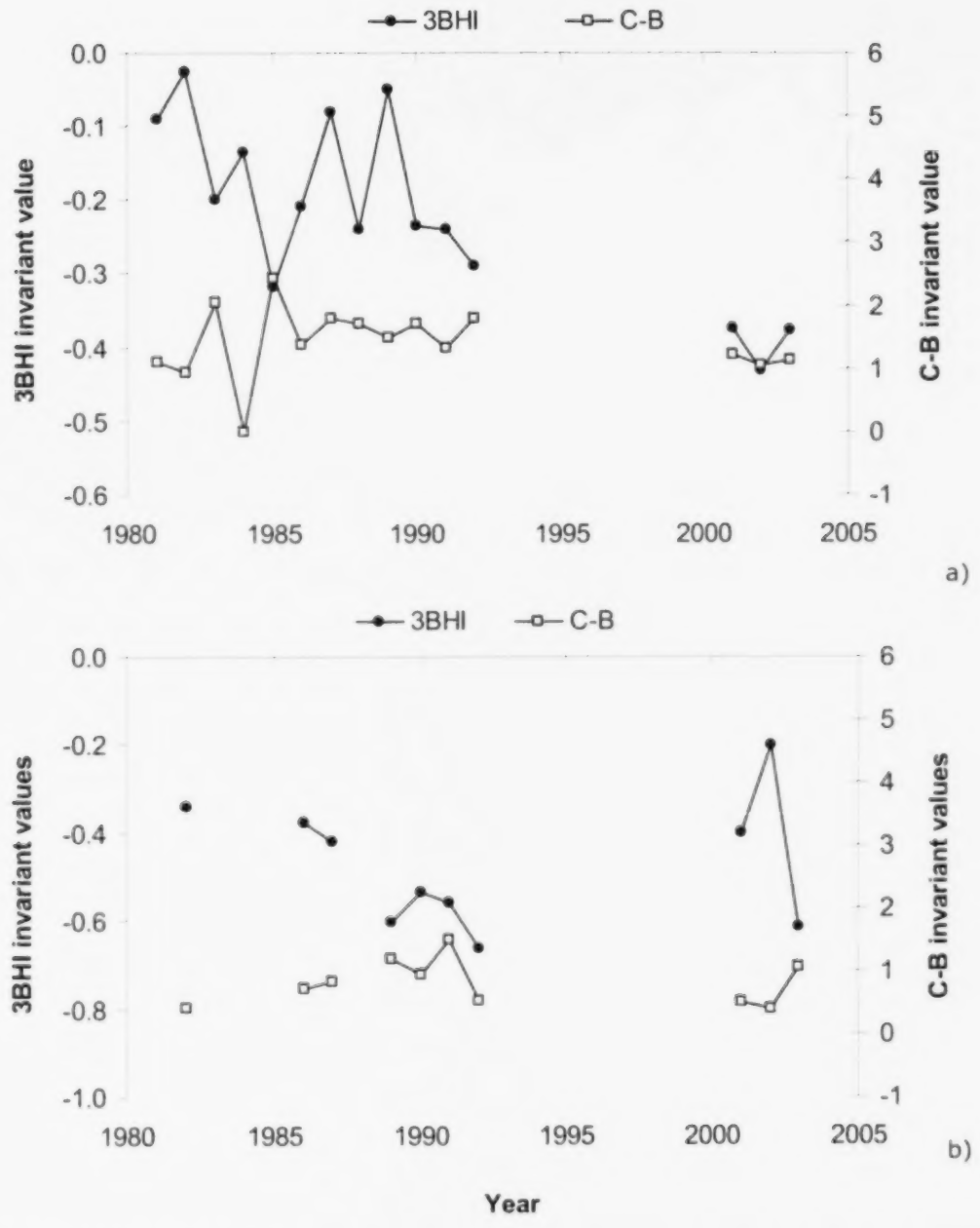

Figure 8. Intrapopulation changes in the 3rd Beverton-Holt (3BHI) and Charnov-Berrigan (C-B) invariants through time for a) lake whitefish in Lake Huron and b) bloater in Lake Erie, population codes are HLWFON2 and EWAL1, respectively. Proposed invariant values are -0.5 for the 3BHI and 2 for the C-B invariant.

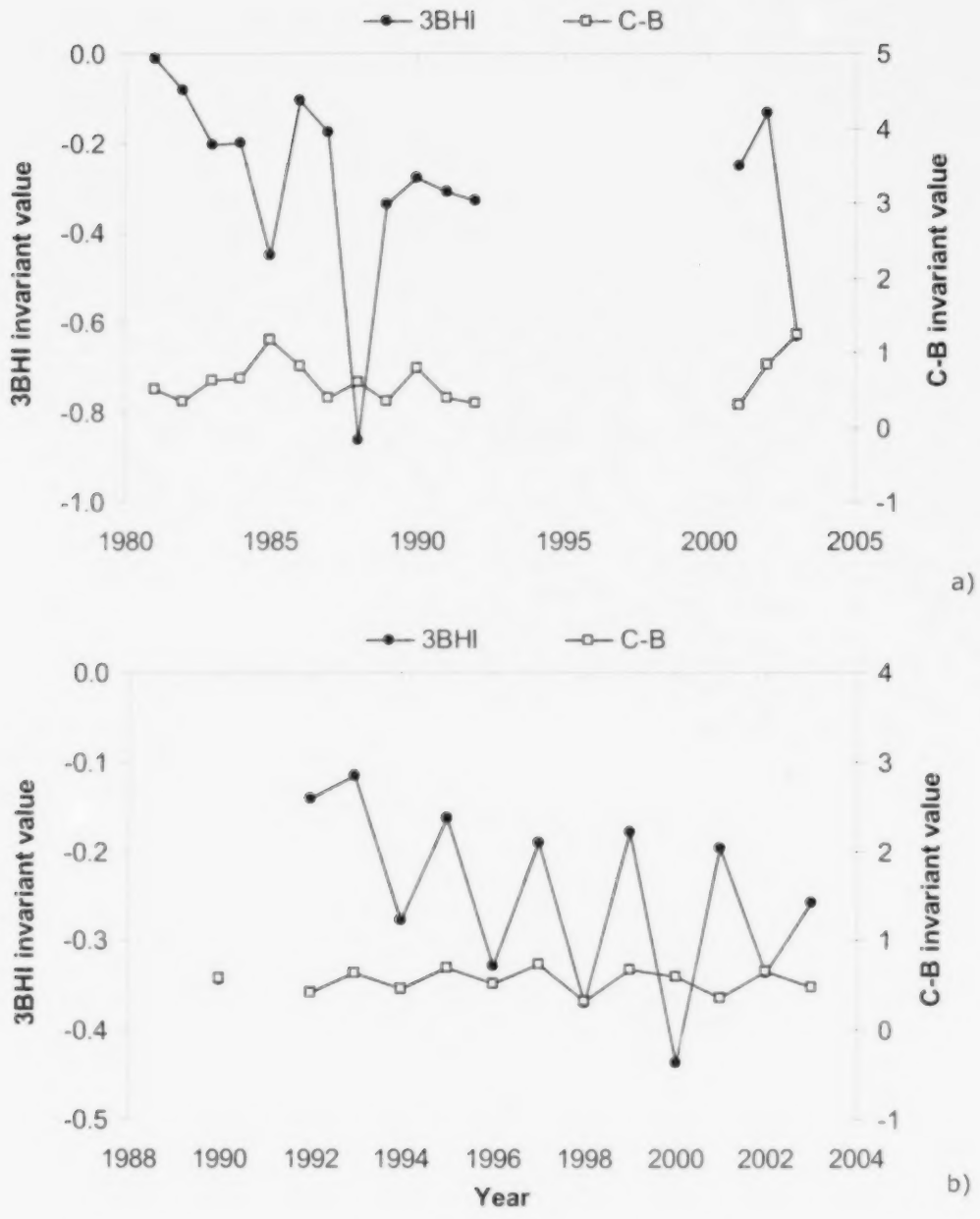

Figure 9. Intrapopulation changes in the 3rd Beverton-Holt (3BHI) and Charnov-Berrigan (C-B) invariants through time for a) yellow perch in Lake Huron, and b) walleye in Lake Michigan, population codes are HYPON2 and HBLOON2, respectively. Proposed invariant values are -0.5 for the 3BHI and 2 for the C-B invariant.